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v. 20
Pt. 1
1963

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The Nature of an Unusual Amino Acid-Pyrimidine Complex from the Cod Parasite, *Porrocaecum decipiens*[1]

BY H. C. FREEMAN, P. L. HOOGLAND[2] AND P. H. ODENSE

Fisheries Research Board of Canada
Technological Station, Halifax, N.S.

ABSTRACT

The proximate analysis of the cod parasite, *Porrocaecum decipiens*, has been carried out. During the determination of the amino acid composition of a hydrolysate of the parasite the presence of an unusual complex was detected as an unknown peak in the amino acid ion-exchange chromatogram. The unknown complex was also found to be present in a protein-free nucleic acid fraction prepared from the parasite. The substance proved to be highly resistant to conventional methods of hydrolysis. Glutamic acid was found to be an end product when the complex was degraded and it is thought that the complex consists of a thymine nucleoside associated with a peptide consisting of three to five glutamic acid residues. It is not known whether the complex is naturally occurring or is an artifact formed during the acid hydrolysis.

INTRODUCTION

IN CONJUNCTION WITH the nutritional experiments of Crampton *et al.* (1960) an analysis of the cod parasite, *Porrocaecum decipiens*, has been performed. The most interesting aspect of the analysis was the appearance of a new pyrimidine complex in the acid hydrolysate of the parasite. This substance interfered with the Spackman *et al.* (1958) amino acid analysis of the parasite by producing a reddish-brown ninhydrin reaction product which gave rise to a peak ahead of aspartic acid in the amino acid chromatogram. The analysis of the parasite, the preparation and the characterization of this substance are reported.

MATERIALS

Porrocaecum decipiens, a member of the nematode phylum, was collected from the muscle of the Atlantic cod, *Gadus callarias*, washed free of adhering muscle, frozen, and stored at –10°C.

Dowex 50 × 4 resin "Baker analyzed" reagent was obtained from the J. Baker Chemical Company, Phillipsburg, N.H., U.S.A.

Resins and chemicals for use with the Beckman/Spinco Amino Acid Analyser were of the quality specified in the Instruction Manual (Spackman, 1960).

Pyrimidine compounds were obtained from the Nutritional Biochemical Corporation, Cleveland, Ohio, U.S.A.

Darco G60 decolorizing charcoal was manufactured by the Atlas Powder Company, 60 East 42nd St., New York 17, N.Y., U.S.A.

All other chemicals used were reagent grade.

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[1] Received for publication April 17, 1962.

[2] Present address: Royal Netherlands Fermentation Industries, Ltd., Delft, The Netherlands.

J. FISH. RES. BD. CANADA, **20**(1), 1963.
Printed in Canada.

METHODS

MOISTURE. The weight lost by preparations kept at 105°C for 15 hr, followed by 1 hr at room temperature in a vacuum desiccator containing P_2O_5 as the drying agent.

NITROGEN. Micro-Kjeldahl: selenium catalyst. Fels and Veatch (1959).

PROTEIN. Nitrogen × 6.25.

FAT. Petroleum ether (B.P. 30 — 60°C) extractables from dry material.

CARBOHYDRATE. Seifter *et al.* (1950).

ASH. Residue at 525°C, method 29:13, A.O.A.C. (1955).

AMINO ACIDS. Spackman *et al.* (1958).

FOLIC ACID. Difco Manual (1958).

TRYPTOPHAN. Spies and Chambers (1949).

PURINE AND PYRIMIDINE TEST. Vischer and Chargaff (1948).

PHOSPHORUS. Allen (1940).

ORCINOL TEST FOR PURINES AND PYRIMIDINES. Massart and Hoste (1947).

PAPER CHROMATOGRAPHY OF PYRIMIDINE COMPOUNDS. Vischer and Chargaff (1948).

ULTRAVIOLET SPECTRA STUDIES. Fox and Shugar (1952), Shugar and Fox (1952).

HYDROLYSIS FOR AMINO ACID ANALYSIS. Approximately 5-g samples of frozen parasite were refluxed with 100 ml of constant boiling hydrochloric acid for 24 hr. Acid was removed by distillation under reduced pressure (repeated three times after the addition of water). The residue was taken up in citrate buffer pH 2.2 ("sample diluent buffer" containing thiodiglycol, BRIJ and octanoic acid, according to Spackman (1960)) and made to volume to obtain a nitrogen concentration of approximately 0.150 mg/ml. Two millilitres of this solution was used on each column.

PREPARATION OF PYRIMIDINE-AMINO ACID COMPLEX (PGC). Fifty grams of freshly frozen cod parasite was refluxed for 24 hr with 500 ml of constant boiling hydrochloric acid. The acid was removed by distillation under reduced pressure (repeated three times after the addition of water). The residue was dissolved in 300 ml of water and treated several times with decolorizing charcoal (Darco G60). The aqueous extract was concentrated on a hot water bath using a slight vacuum and was made up to a volume of 50 ml. One millilitre represents the extract from one gram of parasite.

The crude PGC was isolated using a 2.3 × 40 cm ion-exchange column prepared from Dowex 50 × 4 (200–400 mesh) as follows: the resin was prepared by the method of Moore and Stein (1951) and converted to the hydrogen ion form by washing with $1N$ hydrochloric acid, followed by washing with water until the effluent pH was > 5.0. At the end of each preparative run the column was regenerated by washing with 300 ml of $1N$ sodium hydroxide, followed by 500 ml of $1N$ hydrochloric acid and a final washing with water until the pH was > 5.0.

Ten millilitres of the prepared hydrolysate (from 10 g of parasite) was placed on the ion-exchange column. The column was eluted with water at a flow rate of 0.3 ml/min and fractions containing 4.37 ml were collected using a fraction collector. Fractions containing the PGC were detected by carrying out the ninhydrin reaction (Moore and Stein, 1954) on 0.1-ml samples taken from each fraction or by determining the ultraviolet absorption spectrum of each fraction using a Beckman model DK-2 recording spectrophotometer.

The PGC produced a deep reddish-brown colour with ninhydrin and was found to occur in tube numbers 30 to 40. Fractions containing the compound were combined, concentrated on a hot water bath using a slight vacuum and were purified by descending paper chromatography on Whatman No. 1 chromatographic paper at 20°C using n-butanol saturated with water.

NUCLEIC ACID PREPARATION. The nucleic acid extract was prepared from frozen parasites using the procedure of Littlefield and Dunn (1958) and the chloroform–octanol procedure of Sevag *et al.* (1938) for removing protein which was confirmed by a negative biuret test (Snow, 1950). The preparation was hydrolyzed for 24 hr using constant boiling hydrochloric acid, and any trace amino acids present were removed by column chromatography on a Dowex 50 × 4 (200–400 mesh) column using the same procedure as in the preparation of the crude PGC. The complex was then prepared for amino acid analysis as described for the parasite.

LOCATION OF COMPOUNDS ON CHROMATOGRAM. At times it was difficult to detect the complex on paper because of its hygroscopic nature which caused it to diffuse into the paper. However, if sufficiently concentrated, it could be detected as a dark spot on the chromatogram when viewed under ultraviolet light (260 mμ). When the sample was not required for further work, the spot was made more apparent by spraying the chromatogram with 0.005% fluorescein in 0.5N ammonia which increased the fluorescent background. In high concentrations, the complex could be detected by spraying the chromatogram with ninhydrin. Fortunately, its location on the chromatogram was easily predicted by its proximity to a fluorescent band. The position of the complex was confirmed by carrying out the ninhydrin reaction and by determining the ultraviolet absorption spectrum on aliquots of the aqueous extract of paper cut from the area.

CHEMICAL DETERMINATION OF THYMINE. The PGC was dried over P_2O_5 in a vacuum desiccator and 0.027 g was dissolved in 0.6 ml of 98% formic acid. The solution was sealed into a thick-walled capillary tube, enclosed in a brass guard-tube, and heated at 175°C for 2 hr (Uzman and Desoer, 1954). After hydrolysis the tubes were frozen in dry ice–acetone before opening. The hydrolysate was placed over $CaCl_2$–KOH in a vacuum desiccator to remove formic acid and water and the last traces of acid were removed by extracting the residue with ether. The chemical determination of thymine (Woodhouse, 1949) was carried out on an aqueous solution of the residue.

HYDROLYSIS OF PGC FOR AMINO ACID ANALYSIS. One millilitre of 98% formic acid and 0.3 ml of 30% H_2O_2 were added to the PGC prepared from 0.5 g of parasite. Following the oxidation for 6 hr at 25°C, 15 ml of water was added and the solution was lyophilized. The colourless, viscous, residual liquid was dissolved in 2 ml of 5*N* sodium hydroxide and heated at 100°C for 16½ hr in a teflon test tube. The alkaline solution was neutralized with hydrochloric acid and evaporated to dryness on a hot water bath under a slight vacuum. The residue was made up to 9 ml using pH 2.2 buffer for diluent (Spackman, 1960) and 3 ml was used for amino acid column chromatography.

RESULTS AND DISCUSSION

ANALYSES. The mean value of at least three proximate analysis determinations of each constituent are given in Table I.

The amino acid composition and nitrogen content of a typical acid hydrolysate of the parasite is given in Table II.

TABLE I. Proximate analysis of cod parasite *Porrocaecum decipiens*.

Constituent	Content
	%
Moisture	66.12
Ash	1.11
Fat	0.45
Carbohydrate (expressed as glycogen)	18.70
Nitrogen	2.06
Protein (N × 6.25)	12.9
Tryptophan	0.12

TABLE II. Amino acid and amino acid nitrogen content of *Porrocaecum decipiens*.

Amino acid	g/100 g*	g Nitrogen/100 g*
Lysine	0.93	0.18
Histidine	0.30	0.081
Ammonia	0.19	0.16
Arginine	0.90	0.29
Aspartic acid	1.24	0.13
Threonine	0.55	0.065
Serine	0.52	0.069
Glutamic acid**	1.89	0.18
Proline	0.98	0.12
Glycine	1.07	0.20
Alanine	0.81	0.13
½ Cystine	1.42	0.017
Valine	0.62	0.074
Methionine	0.29	0.027
Isoleucine	0.58	0.062
Leucine	0.82	0.088
Tyrosine	0.37	0.029
Phenylalanine	0.45	0.038

*The contents are expressed on the basis of 100 g of fresh worms.
**Not including glutamic acid in PGC.

Characterization and Identification. It was shown by ion-exchange chromatography that the PGC appeared only after hydrolysis of the parasite. Some of the PGC can be extracted by dialysis of a homogenate of the parasite against water but it was necessary to hydrolyze the extract in order to detect the PGC by column chromatography. The position of the PGC on the chromatogram (Fig. 1) and the pH of the solution of the complex after elution from a preparative column, indicate that the PGC was strongly acidic.

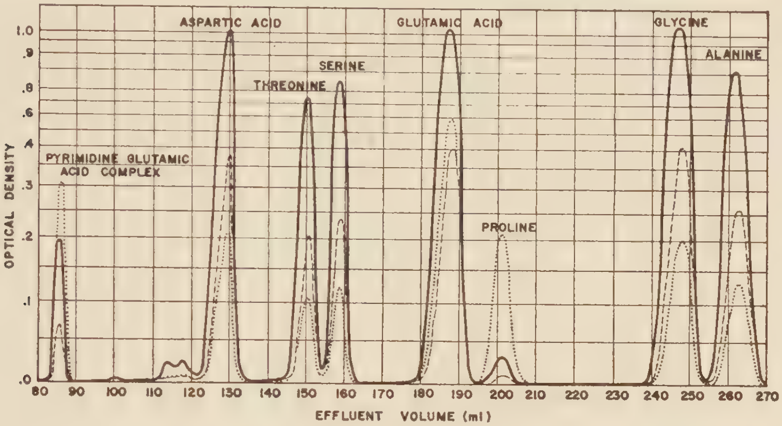

Fig. 1. The position of PGC relative to the amino acids on the amino acid chromatogram.

PGC was not precipitated by protein precipitants such as trichloroacetic acid. Its reaction product with ninhydrin was a reddish-brown colour unlike that of a simple amino acid.

For identification and characterization the PGC was isolated by a combination of column and paper chromatography described above. A yield of 1.4 μM of PGC (based on thymine determination) per gram of parasite was obtained. The ultraviolet spectra of the complex indicate a nucleic acid breakdown product (Fox and Shugar, 1952). These spectra are shown in Fig. 2. The nucleic acid origin of the complex was confirmed when the PGC was prepared from a nucleic acid preparation obtained from the parasite by standard methods.

Paper chromatography of the PGC failed to show the presence of free purines and pyrimidines other than thymine in the preparation. The orcinol test for purine nucleosides (Massart and Hoste, 1947) was negative but after treatment of the PGC with bromine a positive pyrimidine nucleoside test was obtained. The compound was found to contain no phosphorous showing that PGC was not a nucleotide.

Descending paper chromatography of PGC in a butanol–water system showed that the PGC travelled at practically the same rate as thymine and a mixture of PGC and thymine showed no separation. The R_f values of the PGC and thymine were 0.45 and 0.44 respectively. Hotchkiss (1948) has

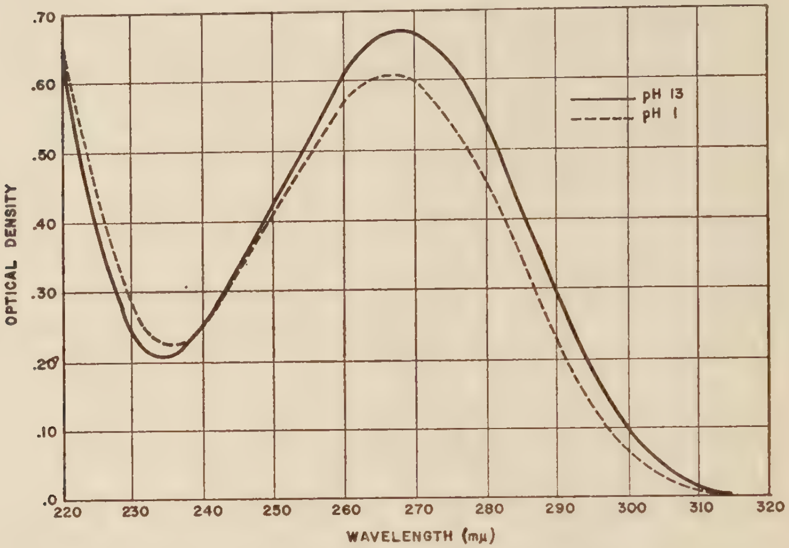

FIG. 2. Ultraviolet absorption of a 62 μM aqueous solution of PGC at pH values indicated (estimated as thymine riboside).

reported that thymidine travels very closely to thymine in butanol–water systems (R_f values of 0.51 and 0.54, respectively). Vischer and Chargaff (1948) reported the R_f of thymine in a butanol–water system as 0.47.

The ultraviolet spectra of PGC (Fig. 2) show maxima at 267 mμ at pH 1, and 268 mμ at pH 13. There was no great shift of the maximum with a change in pH and according to Fox and Shugar (1952) this is characteristic of all glycopyranosyl, ribofuranosyl and deoxyribofuranosyl nucleosides of uracil and thymine. When compared with known spectra (Fox and Shugar, 1952; Littlefield and Dunn, 1958; Dawson *et al.*, 1959) it was seen that the PGC spectrum was very similar to that of thymine riboside which also has a maximum at 267 mμ at pH 1 which shifts to 268 mμ at pH 13. Thymidine, uracil deoxyriboside, uracil pyranoside and uracil ribopyranoside have maxima at 267 mμ, 262 mμ, 259.5 mμ and 262 mμ respectively, which do not shift with pH over the range from pH 1 to 13. The ultraviolet spectrum of the PGC therefore indicated that it contained a thymine compound. The presence of thymine in PGC was confirmed by using the method of Woodhouse (1949) on a concentrated formic acid partial hydrolysate of PGC. This test, which is specific for thymine, was positive.

DEGRADATION OF PGC. In order to explain the ninhydrin reaction of PGC which is not characteristic of nucleosides it was postulated that the PGC was a nucleoside with an amino sugar. Attempts to hydrolyze such a sugar from the base were unsuccessful. All standard and some unusual methods of hydrolysis failed. These attempts included the use of (a) 70% perchloric acid for 1 hr at 100°C, (b) concentrated formic acid for 2 hr at 175°C, (c) 6*N* hydrochloric acid for 96 hr at boiling temperature, (d) 25% sulphuric acid for 2 hr at 100°C, (e) hydrazine method of Barron and Brown (1955), (f) various concentrations of sodium hydroxide up to 10*N* for 16 hr, (g) 70% perchloric acid followed by refluxing with *N* hydrochloric acid for 24 hr, (h) 70% perchloric acid followed by 5*N* sodium hydroxide for 16 hr at 100°C, (i) bromine water at 105°C for 40 minutes followed by hydrolysis with 6*N* hydrochloric acid for 24 hr. Paper and column chromatography were employed to detect the hydrolysis products but in all cases the PGC was not affected by the treatment or was only slightly degraded. One method proved partially successful. Using a modified procedure of Haavaldsen *et al.* (1959) the PGC was made alkaline and reduced for several days with 3% sodium amalgam, then hydrolyzed 24 hr with constant boiling hydrochloric acid. Column chromatography of the hydrolysate failed to demonstrate the presence of any amino sugar but glutamic acid appeared unexpectedly as a hydrolysis product. The presence of glutamic acid in the hydrolysate was confirmed by paper chromatography.

It was also found possible to detach most of the glutamic acid residue by oxidation of the PGC for 6 hr with performic acid at 25°C (Hirs, 1956) followed by a 16½ hr hydrolysis using 5*N* sodium hydroxide at 100°C in a teflon tube. This treatment caused considerable degradation of the glutamic acid to aspartic acid, serine and glycine as shown in Fig. 3.

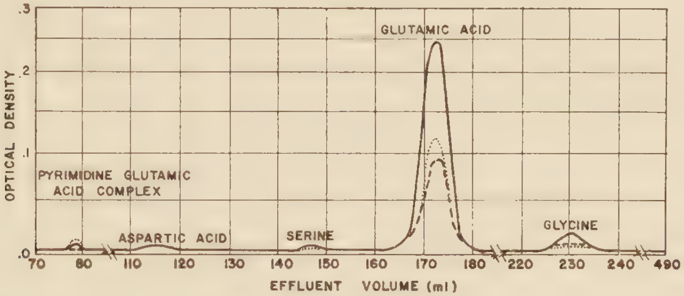

FIG. 3. Amino acid chromatogram showing the disappearance of most of PGC and the appearance of serine, aspartic acid, glutamic acid and glycine after oxidation with performic acid for 6 hr at 25°C followed by treatment with 5*N* sodium hydroxide for 16½ hr at 100°C. Only 0.5% of the PGC originally present was not degraded.

The origin of these amino acids in the chromatogram was confirmed by subjecting chromatographically pure glutamic acid (see Fig. 4) to the same treatment and then chromatographing the hydrolysate whereupon these amino acids again appeared on the chromatogram in the same proportions as shown in Fig. 5.

PRODUCTS OF DEGRADATION. The approximate molar ratio of thymine to glutamic acid in PGC was determined. The concentration of thymine was determined by its ultraviolet absorption, using the molar extinction coefficient of thymine riboside for the estimation (Dawson *et al.*, 1959). Degradation studies were used to determine the glutamic acid content. It was found that 0.570 μM of PGC (based on thymine concentration) yielded 2.06 μM of glutamic

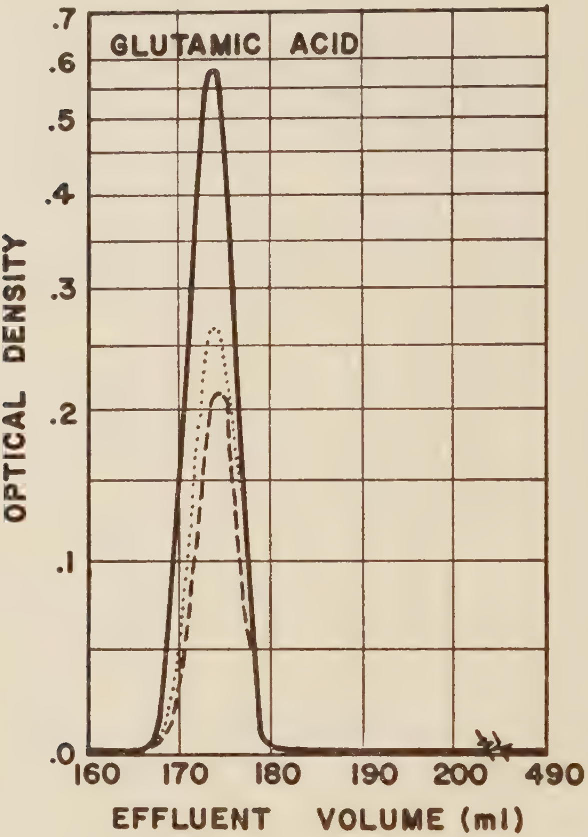

FIG. 4. The amino acid chromatogram of one μM of glutamic acid.

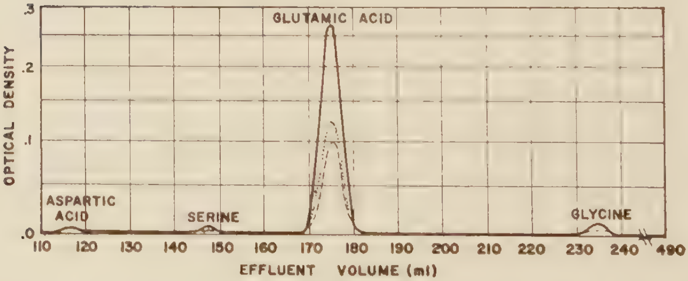

FIG. 5. The amino acid chromatogram of 0.67 μM of glutamic acid after oxidation with performic acid for 6 hr at 25°C followed by hydrolysis with 5*N* sodium hydroxide for 16½ hr at 100°C showing the breakdown of glutamic acid to form glycine, serine and aspartic acid.

acid after performic acid oxidation followed by $5N$ sodium hydroxide hydrolysis. It was also found that destruction of glutamic acid occurred during the treatment and that some of the PGC was not hydrolyzed. This was demonstrated by carrying out degradation studies on the PGC alone and on PGC samples to which known amounts of glutamic acid were added prior to treatment showing that the added glutamic acid tended to suppress the hydrolysis of the PGC. However, when allowances were made for hydrolytic losses and incomplete hydrolysis, it was estimated that one mole of the thymine compound was associated with a glutamic acid peptide containing 3 to 5 glutamic acid molecules.

STRUCTURE AND ITS RELATION TO STABILITY AND NINHYDRIN COLOUR. It is unusual for peptides to be so resistant to hydrolysis. Consden *et al.* (1947) found peptides containing proline to be unusually stable which was presumed to be due to steric factors. They also found the cyclic peptide "gramicidin S" to be fairly resistant to acid hydrolysis. The unusual stability of cyclic structures has also been clearly demonstrated by Swanson and Cori (1948) who showed that cyclic Schardinger dextrins are considerably more stable than corresponding open chain polysaccharides. It was suggested by Sanger (1952) "that immobilization of the peptide bond from rotation may be an important factor in inhibiting hydrolysis". He reported that such an effect might account for the stability of proline peptides.

The dark reddish-brown color that PGC formed with ninhydrin may be attributed to its reaction with free imino groups in the glutamic acid polymer. A similar brownish reaction product with ninhydrin is formed by proline (pyrrolidine carboxylic acid) and hydroxy proline (hydroxy-pyrrolidine carboxylic acid). It was shown by Vickery *et al.* (1935), Moore and Stein (1951) and Wiltshire (1953) that glutamic acid and also glutamine are converted under specific conditions to the anhydride of glutamic acid, pyrrolidone carboxylic acid. All of the aforementioned cyclic compounds have a common nucleus with a common imino group. It is thought that possibly the glutamic acid peptide may exist in PGC as a pyrrolidone carboxylic acid polymer having some free imino groups. If this were so, it would explain the formation of the reddish-brown color with ninhydrin and account for its unusual stability.

COMPARISON TO SIMILAR COMPOUNDS. The PGC bears a superficial resemblance to folic acid, and related pteroylglutamic acid compounds but a negative result was obtained when it was tested for folic acid activity using the microorganism *Streptococcus fecalis* ("*S. lactis* R") No. 8043 (American Type Culture).

The PGC also bears a slight resemblance to the unusual adenine-succinic acid-peptide compound isolated from salmon liver by Tsuyuki and Idler (1957) which also gave a positive ninhydrin test and had an ultraviolet absorption maximum at 266 mμ in acid medium; however, there was a great difference when the chemical composition and stability of the two compounds were compared.

CONCLUSION

It is thought that the interfering substance which appeared on the amino acid chromatogram during the amino-acid analysis of the cod parasite, *Porrocaecum decipiens*, is a thymine nucleoside associated with a glutamic acid peptide.

It is not known whether the complex is naturally occurring or whether it is an artifact. The PGC was found to be stable to most of the methods of chemical treatment described and all attempts to separate the complex into its intact components were unsuccessful.

ACKNOWLEDGMENT

The authors wish to acknowledge the valuable technical assistance of Mr A. E. Waddell.

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Sampling the Catch of a Research Vessel[1]

By J. E. Paloheimo and L. M. Dickie

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

The sampling procedure commonly used on board research vessels in which catches are sorted by species and picked up into baskets was examined in catches containing several species, principally haddock. The procedure does not appear to permit withdrawal of random samples for lengths or counts of fish. Mixing these basket lots results in sample units which are effectively homogeneous for length composition and reduces the amount of sampling necessary to estimate numbers of fish caught. However, mixing does not appear to be effective if the species sort is omitted, especially in large catches.

INTRODUCTION

Research vessels are frequently used to sample natural fish populations free from the bias which may be introduced into commercial catch samples by the special practices of fishermen. However, this method of study often results in the taking of a large number of relatively large research-vessel catches. The complex of observations which must then be made on each catch inevitably requires deck sampling if the time of the research vessel is to be used effectively. A necessary early step in the planning of programs and operating procedures on the vessel is a study of the nature of the variation among the sample units to be used.

While one has the impression that this sampling problem has been the subject of rather wide study in fisheries, most of the publications which have come to our attention are devoted to studies of analogous problems in the sampling of commercial landings (e.g. Gulland, 1955). An exception is the work reported by Pope (1957), who has studied the variability in average lengths among sampling units, and the reliability of estimation of average length from fixed-ratio sampling within all sampling units. This procedure requires handling of all fish in each of the sampling units in the catch, and could not be readily applied to the situations we encountered in which catches were frequently large. We have therefore investigated the effects of various handling procedures on the randomness of selection for species, lengths and total numbers caught, when only a fraction of the sample units were to be handled.

The project was suggested by Dr W. R. Martin, scientist in charge of the Groundfish Investigations at the Biological Station, St. Andrews, N.B., and was carried out in February 1960 on the Fisheries Research Board of Canada's research vessel *A. T. Cameron*. During the experiments the authors were

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[1] Received for publication April 25, 1962.

J. Fish. Res. Bd. Canada, **20**(1), 1963.
Printed in Canada.

fortunate in having the vessel operations under the especially competent direction of Captain B. Blackwood and his First Mate, Mr C. Pardy. The deck handling program was supervised by Mr D. N. Fitzgerald and Mr P. M. Powles, assisted by Messrs C. Bayers, M. Fraser, E. Fevens and G. Mann, all members of the scientific and technical staff of the St. Andrews Station, and by the crew of the vessel. The authors wish to thank these men for the excellent performance of the arduous tasks which fell to their lot. We also wish to express our appreciation of the additional assistance rendered by Mr G. Mann and Mrs I. Thompson in the calculations involved in the analysis.

PROCEDURE

A network of 41 stations was set up in a 2500 square mile area on Western and Emerald Banks of the Scotian Shelf. The positions of the stations, shown in Fig. 1, were chosen randomly from the 100 squares, each 5 by 5 nautical miles, into which the whole area was divided; half-hour tows were made close to the centre of each square. About half of the stations were randomly chosen as

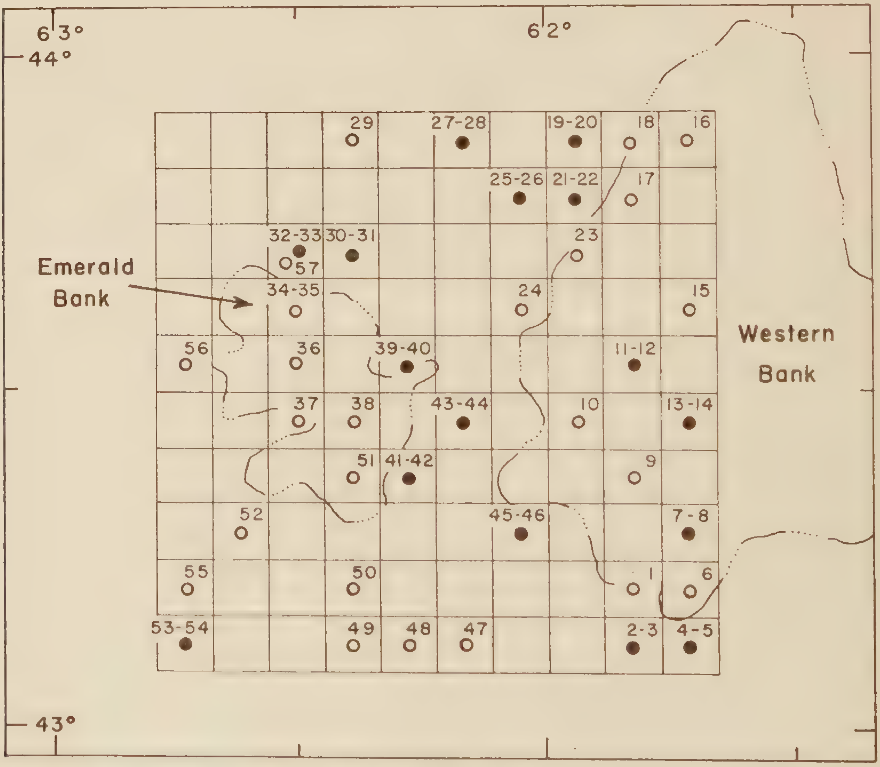
63°
62°
44°
43°
Emerald Bank
Western Bank
29
27-28
19-20
18
16
25-26
21-22
17
32-33
30-31
57
23
34-35
24
15
56
36
39-40
11-12
37
38
43-44
10
13-14
51
41-42
9
52
45-46
7-8
55
50
1
6
53-54
49
48
47
2-3
4-5

FIG. 1. A chart of part of the central Scotian Shelf showing the area surveyed by the *A. T. Cameron* deck-sampling cruise. Tow numbers are shown beside circles marking approximate station positions. Single-tow stations are open circles; double-tow stations are filled-in circles. The 50-fathom depth contour is shown.

double-tow stations. Altogether 61 tows were made. Results of four of them were rejected because the net was torn or fouled. Results of the remaining 57 tows are used in this analysis of the deck sampling.

The fishing net was a large otter trawl (Yankee 41-5; headrope of approximately 80 ft or 24 m) with a small-mesh codend liner ($1\frac{1}{8}$ inches or 29 mm between knots). Catches, especially of haddock, were frequently large (more than 1500 lb or 700 kg per half-hour tow).

At each station the catch, which had been dumped into the fish pen on deck, was either sorted into species and picked up into baskets, which held about 75 lb (34 kg) of fish each, as had been done routinely on other survey cruises, or else it was picked up into baskets without an initial species sort. An exception was made for all very large fish, which were removed from the catch and handled separately, partly because of the special interest in making observations on these relatively rare specimens, and partly because they are not readily handled in the baskets. The numbers and length compositions of all the fish in a basket were recorded separately by species but in what follows a basket sample is defined as all fish in the basket. In most cases records were kept for each basket sample in the catch. After the recording by baskets was complete the contents of each of the baskets were then frequently divided among several large boxes (about 250 lb or 114 kg capacity). This was accomplished by dumping approximately one-fifth of a basket at a time into successive boxes. No attempt was made to sort fish individually into the boxes. The species numbers and length compositions of these mixed basket samples were recorded as box samples; a box sample consisted of all fish in the box. In some cases only basket or box sample units were used. The effects of various other procedures for employing the basket sample units were also examined, including stratification of the order in which they came from the pen, or according to a rough sort by size (usually equivalent to species).

SAMPLING FOR LENGTH COMPOSITIONS

a. POOLED RESULTS. To test the reliability of the sampling units for representing the length composition of the catch, the lengths of fish in each sample unit were grouped into 10-cm length classes (10–19, 20–29, etc.), except when these class intervals resulted in many small numbers. In these cases 20- or 30-cm length classes were used. Standard tests were made for homogeneity of variation among parallel sample units (Rao, 1952); that is, the records of length composition of the sample units from the catch were arranged in a 2-way table from which marginal totals of the numbers of fish in each length group and each sample lot could be obtained. Marginal totals were used to calculate the expected length-frequency distributions for each of the sample units, and the χ^2 test for homogeneity of the samples was carried out in standard fashion, where:

$$\chi^2 = \Sigma \frac{(O - E)^2}{E} = \Sigma\ (O^2/E - O)$$

and where "O" is the observed and "E" the expected frequency in each category.

Table I presents a sample set of data and calculations for a test of the homogeneity of the length composition in basket lots of the haddock catch in the first tow of the cruise. In this tow, the total haddock catch was 10 baskets, although the length-composition record for one of these was afterwards lost. Before calculating the χ^2 value, the 9 remaining separate basket lots were grouped randomly into pairs (in this case 4 pairs and 1 single basket), and the paired basket lots were treated as the sample units. The χ^2 calculated for this example was 61.7, which was assigned 16 degrees of freedom (d.f.) rather than 20 because the horizontal totals were an estimate of the true total for the catch. The χ^2/d.f. value indicates significant departure from the hypothesis that the paired basket lots were random samples of the deck catch. The test was repeated using the 9 basket lots grouped randomly into threes. The resulting calculations yielded a $\chi^2 = 80.7$, which with 8 degrees of freedom indicates that there was also a highly significant departure from randomness in the larger sized sample units.

TABLE I. Table of observed and expected length frequencies in parallel sample lots of the haddock catch taken in Tow 1, *A. T. Cameron* Cruise No. 18, as a basis for a χ^2 test for homogeneity among the samples.

Basket lot no.	2+6		4+1		9+3		7+10		5		Totals
Length group	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	
cm											
10–19	22	14.3	0	8.8	27	15.9	4	12.0	6	8.0	59
20–29	26	18.2	6	11.2	18	20.2	7	15.2	18	10.2	75
30–39	71	79.9	43	48.9	92	88.7	77	66.9	46	44.6	329
40–49	39	45.2	43	27.7	42	50.1	43	37.8	19	25.2	186
50+	7	7.3	9	4.5	4	8.1	7	6.1	3	4.1	30
Totals	165	...	101	...	183	...	138	...	92	...	679
$\chi^2=\Sigma\left(\frac{O^2}{E}-O\right)$[a] ...		9.4	+	21.0	+	11.4	+	11.7	+	8.2	= 61.7
										(d.f.	= 16)

[a] Figures include correction for continuity.

A total of 32 similar tests were carried out on grouped basket sample lots from all the appropriately handled tows made during the cruise. The pooled χ^2 value was 803.0 with 351 degrees of freedom (see total for basket comparisons, Table II). This confirms the conclusion reached above that there was a highly significant departure from randomness among length compositions of basket-sampling units. By contrast, 45 similar comparisons of all box-lot samples drawn after the initial basket lots were mixed yielded a pooled χ^2 value of 282.3 with 258 degrees of freedom (Table II), indicating no significant departure from

TABLE II. Values of χ^2 and the corresponding degrees of freedom derived in tests for homogeneity of the length composition of parallel samples drawn from different sized catches handled in different ways (Sm = < 750 lb; Md = 750–1,500 lb; Lg = > 1,500 lb).

Handling procedure	Sample unit	Size of catch	Cod		Haddock		Other species[a]		Totals for species		Unsorted species	
			χ^2	d.f.	χ^2	d.f.	χ^2	d.f.	χ^2	d.f.	χ^2	d.f.
Initial species sort	Baskets	Sm	...	...	309.0	93[b]	...	...	309.0	93[b]	...	...
		Md	...	...	39.0	18[b]	...	...	39.0	18[b]	...	...
		Lg	...	...	247.7	76[b]	...	...	247.7	76[b]	...	...
	Totals		...	...	595.7	187	...	...	595.7	187	...	...
	Boxes	Sm	3.5	8	38.9	50	...	...	42.4	58	...	...
		Md	...	...	39.2	38	...	...	39.2	38	...	...
		Lg	2.0	4	40.8	31	...	...	42.8	35	...	...
	Totals		5.5	12	118.9	119	...	...	124.4	131	...	...
No initial species sort	Baskets	Sm	...	...	0.2	2	13.4	22	13.6	24	8.3	10
		Md	...	...	48.0	33[b]	80.7	70	128.7	103[b]	280.7	70[b]
		Lg	...	...	65.0	37[b]	...	...	65.0	37[b]	185.2	50[b]
	Totals		...	...	113.2	72	94.1	92	207.3	164	474.2	130
	Boxes	Sm	...	...	5.2	15	3.1	3	8.3	18	21.6	13
		Md	...	...	36.9	21[b]	34.5	30	71.4	51[b]	42.9	30
		Lg	...	...	39.0	26[b]	39.2	32	78.2	58[b]	68.4	32[b]
	Totals		...	...	81.1	62	76.8	65	157.9	127	132.9	75
							Total for baskets		803.0	351		
							Total for boxes		282.3	258		

[a] Includes measurements of redfish, flounders (mostly American plaice), pollock and herring.
[b] $P > 95\%$.

randomness. We may conclude that a simple procedure for mixing the basket lots was sufficient to ensure random sampling for the length composition of the catch.

b. EFFECTS OF SPECIES AND AMOUNT OF CATCH. The pooled χ^2 values for the basket and box units include comparisons of length-frequency distributions within several different species for different sizes of catches, either with or without an initial species sort. It is evident that these different components will not make equal contributions to the overall result. Since with the present deck design and equipment of the *A. T. Cameron*, basket-lot handling is the most convenient procedure yet tried, and subsequent mixing is somewhat more laborious, it is of great practical importance to isolate and study these effects of species and size of catch on the pooled total. Thus, the tests from various tows have been classified as shown in Table II. The results provide a basis for determining if there are particular conditions under which the basket-handling procedure can be used directly.

All catches were classified into size categories according to weight. In Table II these have been called:

Small:	less than an estimated 750 lb (341 kg)	per half-hour tow
Medium:	between 750 and 1500 lb (341–682 kg)	" " " "
Large:	over 1500 lb (682 kg)	" " " "

Within each size-class of catch, basket- and box-sampling units of separated and mixed species were examined.

Table II shows that catches of fish species other than haddock were generally small throughout the cruise. Hence, most of the conclusions about the adequacy of the usual deck procedure of sorting the species into baskets are well established only for the haddock. From the first part of the Table (i.e. for species sorts) it appears that increasing sizes of catches of haddock did not result in any appreciable change in the heterogeneity among lengths in the basket sample lots, whereas mixing these basket lots into boxes and then sampling successfully reduced the heterogeneity among samples of all sizes of catch to the point where all may be considered as random samples. It is apparent that without such a restriction as mixing on the design of the deck procedure, basket lots of individual species chosen randomly from the sorted deck catch cannot be used to give unbiassed estimates of the size composition in any size of catch.

Initial sorting of the catch into species takes an appreciable fraction of the total time required for the deck handling. We therefore examined the length-composition samples of particular species, and of all species together, when the catch was picked up without an initial species sort. The results for both basket- and box-sample units when the initial species sort was omitted are shown in the lower part of Table II. The χ^2 values for haddock in basket-sample units indicate that the procedure of picking up the fish without a species sort failed to give homogeneous samples of the length compositions in medium- and large-sized catches. This conclusion is confirmed by the χ^2/d.f. values for basket lots of mixed species. The χ^2 value for one small catch indicates no significant heterogeneity for either haddock or other species included in it. However, this result is based on a catch in which the numbers of haddock caught were so small that considerable lumping was necessary for the calculation. The resulting χ^2 with only 2 degrees of freedom is an insufficient basis for generalization.

From the remaining data in the lower half of Table II it appears that, with omission of the species sort, the length compositions of haddock in the box-sample units were no longer homogeneous, at least in the medium- and large-sized catches, and a similar result was obtained for mixed species in large catches. It is apparent that mixing of the basket lots in boxes was not accomplished as effectively when the baskets contained several species, as when the species were treated separately. From the results with mixed species it appears furthermore that the mixing may have been less effective in the large than in the smaller catches.

c. STRATIFICATION OF BASKET LOTS ACCORDING TO THE ORDER OF FILLING. It is frequently stated that one of the reasons why it is so difficult to get representative samples from a pile of fish is that during any disturbance of the pile the smaller fish tend to slip towards the bottom, leaving the larger fish to be picked off the top first. This effect is quite evident to anyone watching fish being sorted, and can often be seen in the gradation in average sizes of fish in the baskets as they come in sequence from the deck pen. If this be generally true, it may be possible to reduce the heterogeneity among sample units by stratifying these units according to the order in which they come from the pen and then sampling within these strata.

The value of this method of restricted basket-lot sampling was tested for the *A. T. Cameron* deck catch on 3 large catches of haddock (tows 33, 42 and 51, yielding respectively 33, 30 and 14 baskets of haddock). Basket lots were grouped into fives, in the sequence in which they came from the deck pen, and length compositions for each basket lot recorded separately. χ^2 tests for homogeneity were then calculated within each 5-basket lot, and the result compared with the totals between groups. The pooled χ^2 for the within-group comparison was 272.3 with 110 degrees of freedom, compared with 490.7 with 46 d.f. for the between-group comparison. That is, the heterogeneity within strata was very much less than it was between them. However, even with this improvement, there is still significant departure from randomness within basket-sample units of individual strata.

During the series of tests it emerged that, in accordance with expectation, the last group of baskets in the sequence introduced a major proportion of the apparent heterogeneity, since the smallest fish tend to be the last picked up, and most of them may occur in only one or two of the baskets of this final group. As an indication of this effect, it was found that the final basket groups contributed a χ^2 of 127.9 with only 15 d.f. to the total within groups. However, the remainder, 144.4 with 95 d.f., still indicates significant departure from homogeneity within the groups first picked up. With the deck procedure used there was no way to predict whether any one of these first-filled groups of baskets would be likely to contribute the major share of this heterogeneity; nor could particularly aberrant groups be detected by inspection of the groups of baskets on the deck. Sampling of baskets within strata defined by sequence of filling is evidently an insufficient restriction on the handling procedure for assuring random sampling for lengths.

d. STRATIFICATION BY SIZE-GROUPS. Another possible restriction on design which might be incorporated into the convenient basket-lot system would be assortment into rough size categories. This method is the basis on which many commercial firms handle their catches. It is therefore frequently made use of in the sampling of commercial landings. This handling procedure was examined only incidentally by two of the procedures used during the cruise. First, as noted earlier, since only a rough size sort is possible on the deck, very large fish were picked out of the pen and treated separately in most tows. They were usually few in number, and random assortment among baskets was virtually an impossibility. Their presence in baskets also made handling more difficult. In the above comparisons we have thus already removed the effects of very large specimens on our χ^2 tests of homogeneity.

Secondly, the range of size-classes to be examined in a particular test is generally reduced by the species sort. Preliminary information on the effects of size stratification is therefore given by a comparison of χ^2 values for length compositions of "mixed" fish found in sample units where there has been no species sort, with those of the individual species in these mixtures. Such comparisons may be made from Table II.

As might be expected, Table II indicates that with no species sort χ^2/d.f. values were generally higher for the mixture of species than for the individual species in these mixtures. This suggests that sorting by species does in fact decrease heterogeneity by reducing the size range. This suggestion is supported by a comparison of various species in the mixtures. Thus, the χ^2/d.f. values for haddock, which were represented in the catch by a larger range of sizes than were other fish, were greater than were those for other species, and when the species sort was omitted, lengths of these other species appeared to be randomly assorted among both basket- and box-sampling units. The species which generally have a larger size range than haddock were infrequent in all catches, so that our data do not permit further examination of this possibly promising approach to sampling.

In the case of our principal species, haddock, it was clear that size stratification would require a sort which would break well into the size range usually represented in the catch. Any such special handling seemed likely to require time and effort equivalent to that required by the mixing. Since the latter procedure appeared less liable to mismanagement, it was given priority in the study.

How Many Fish to Measure

In most cases investigators using research vessels are interested in obtaining the length-frequency composition at least for each of the commercially-important species in the catch. Given that some method is adopted which permits random sampling for lengths, he then wishes to know how many fish to measure. This problem is a well recognized one in statistics and sampling (c.f. Pope, 1956), and is included here for the sake of completeness.

The investigator will usually be most interested in estimating the relative strength of particular length classes — those representing a particular year-class for example. If we let "p" be the probability that a fish from the sample will be in this class (i.e., the relative (length) frequency), then the standard deviation, s, of our estimate of the relative class strength is given by:

$$s = \sqrt{\frac{pq}{n}(1-a)} = \sqrt{\frac{p\,(1-p)}{n}(1-a)}$$

where n is the total number of fish to be measured in the sample, and $a = n/N$ where N is the total number of fish in the catch. For large catches a is small and the term $\sqrt{1-a}$ approaches 1.

It may be noted that for any relative frequency p, $0 \leq p \leq 1$, the term $p\,(1-p) \leq \frac{1}{4}$, and $\sqrt{p\,(1-p)} \leq \frac{1}{2}$. Hence, in large catches the accuracy, measured by $2s$, is always better than $\pm 2 \times \frac{1}{2}\sqrt{1/n}$, or better than ±7.0% for a sample size $n = 200$ fish. For $n = 300$, the upper bound for the error limits decreases from ±7.0% to ±5.8%. For groups of fish well represented in the catch, the error limits are considerably smaller. For instance, for $p = 0.10$ and $n = 200$, the limits are ±4.4% rather than ±7.0%.

When the catch is small and the investigator samples a fair proportion of the total catch, the accuracy of measurement is appreciably improved over that for large catches. If, for example, the total catch (N) were only 500 fish out of which 200 fish were sampled, the upper bounds for the error limits would be reduced from large sample limits by the factor $\sqrt{1-a} = \sqrt{1-200/500} = 0.78$, or by 22.0%. For a sample size $n = 300$ out of 500 fish, the corresponding reduction would be 37.0%.

The accuracy of estimation required by the investigator and indeed the stratifications he wishes to make will depend upon his use for the data. If only length compositions are required, accuracies of the order afforded by samples of 200 should usually be satisfactory. However, in some cases, as in our large catches, it may be difficult to obtain random samples containing as few as 200 fish. There will then be practical reasons for increasing this number to 300 or more, with the attendant small increase in the accuracy of the estimates, provided always that the samples are random.

A common extension of procedures of sampling for length composition will be the determination of the frequency distribution of various biological characteristics, such as ages, sexes, stages of maturity or stomach contents. Should the sampling for lengths be random, it follows that the length-classes themselves may be sub-sampled for the biological characteristics. The accuracy afforded by the sub-sampling is then calculated by the above equation, with p, n and N referring either to the length-class, or to the whole catch, depending on whether one enquires about the accuracy of the sub-sampling from the length-class, or of the sampling from the whole catch.

As was found in sampling for lengths, it may occasionally be difficult to sample the entire catch randomly for the additional characteristics if only 200 fish are included in the sample. Two alternatives are then open. One is to increase the sample size, as in the length-sampling scheme. The second, preferable alternative is to treat the length-classes (or other groupings) as separate strata of the catch and draw samples independently from each of them (Ketchen, 1950). If it is important only to establish the dependence of the particular characteristics on size, it is not necessary that the length-classes themselves be drawn randomly from the catch, but only that sampling within each class be random. This device of stratified sampling will usually permit satisfactory characterization of the catch with fewer measurements than would otherwise be required. Relative accuracy of the measurements is determined as above.

SAMPLING FOR SPECIES COMPOSITION

When a catch is not predominantly of one species, some time in handling it may be saved by sampling the whole catch without resorting to an initial species sort. As a means of testing whether the species composition could be reliably judged by sampling with the units employed here, we studied the counts of numbers of individuals of each species in the basket or box lots of unsorted species. Since the basket lots turned out to be non-random samples of lengths, it was expected that the same would be true for the species composition as well. This was verified by the analysis. What was not anticipated was that the box lots from all sizes of catches were also non-random samples of the species composition. Pooling the tests, the results indicated that for baskets the χ^2 was 115.8

with 71 d.f., while for boxes it was 232.5 with 148 d.f. Both χ^2 values indicate a significant deviation of the species composition from randomness, despite the fact that in small- and medium-size catches the length composition for boxes of the unsorted species did not show such heterogeneity. It therefore appears that species sorting is to be preferred to mixed species handling, if sampling is to be effective.

HOW MANY FISH TO COUNT

Catches of particular species are frequently large and, given an initial species sort, it may be advisable in the interests of efficient operation to sample for total numbers caught as well as for length composition and other catch characteristics. The number of sampling units which must be counted to achieve given accuracy will, of course, depend upon the size of catch and on the variability among the units. In our case, determination of the required amount of sampling could not be readily made by the usual statistical methods because the basket counts varied in a quite irregular fashion.

Since for many of our tows we know the "universe" completely, it would be theoretically possible to list all of the average basket counts possible in randomly-chosen samples of 1, 2, 3, etc., basket lots. The statistical distribution of average counts could thus be determined from the observations for each level of sampling and a statement made about how many basket lots would have to be counted to have the estimated average fall within certain error limits of the true average in a given percentage of cases. However, the labour of complete enumeration is prohibitive for even moderately large tows; for instance, a sample of 8 baskets can be drawn from a total catch of 33 baskets in:

$$\binom{33}{8} = \frac{33!}{25!\,8!} \approx 1.4 \times 10^7$$

different ways. It is therefore necessary to resort to sampling for the distribution of average counts. This type of technique is usually referred to as "Monte Carlo" sampling. The procedure as used here is applicable to determination of sample size when no assumptions are made about the shape of the parent statistical distribution.

In our application we have made the *a priori* decision that a sample size of m baskets is adequate when the estimated mean basket count falls within 10% of the true (population) mean in at least 90% of cases.[2] That is, $m = 8$ baskets would be an adequate sample of 33 baskets if 90% of the 1.4×10^7 possible average counts were within 10% of the known mean count per basket.

Let us call a sample of size m a "failure" if it yields an estimate of average count outside the 10% limits and a "success" otherwise. To establish whether m baskets is an adequate sample size, we must then draw successive samples of m baskets each and observe the ratio, q, of failures to total trials. This ratio follows the binomial distribution. When it appears that q and also its upper, say 90%, binomial limit are less than 0.10, we know with probability 0.90 that our sample size is adequate. Similarly, when q and its lower 90% limit are higher than 0.10, we know (with probability 0.90) that the sample size is inadequate.

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[2] It is a coincidence that these percentages total 100%.

In determining the smallest adequate sample size we have usually sacrificed statistical rigour for practical expediency and consulted binomial tables only for critical sample sizes. As an example, we have given in Tables III-A and III-B the results of application of this method to determination of the sample size required to estimate the numbers of haddock in Tow 33 of the cruise. As is shown in Table III-A, 33 baskets of haddock were taken in the catch, giving a total of 705 haddock, or an average of 21.4 per basket. The test for homogeneity of the length composition among baskets yielded a χ^2 of 26.5 with 20 degrees of freedom, indicating effectively random assortment of sizes among sample units. Even so, the counts of individual baskets ranged between 12 and 49, and, 26 out of the 33 baskets contained numbers of fish which were outside the 10% limits of 19.2 and 23.5 for average count. With such a distribution it is apparent that a rather large sample size has to be drawn to meet our criterion of adequacy of estimation of numbers caught.

TABLE III-A. The frequency distribution of numbers of haddock in basket samples from Tow 33 in which the test for homogeneity of length compositions yielded $\chi^2 = 26.5$, d.f. = 20. x = count per basket, f = number of baskets.

x	f	x	f	x	f
12	1	19	2	26	1
13	1	20	0	27	0
14	0	21	5	28	1
15	2	22	1	30	1
16	3	23	1	32	1
17	4	24	3	37	1
18	4	25	0	49	1

$\Sigma xf = 705$ $\Sigma f = 33$ $\bar{x} = 21.4$

10% limits of $\bar{x}$ = 19.2 and 23.5

In the example of Table III-B we have begun sampling using sample sizes of 8 baskets. A set of 15 random drawings of 8 baskets each resulted in 9 "successes" and 6 "failures", giving an estimate of $q = 0.40$. Tables of binomial limits (Mainland *et al.*, 1956) indicate that for 6 out of 15 items, q has a 90% probability of lying between 0.22 and 1.00. Obviously the number of failures from a sample size of 8 baskets is far too high for this level of sampling to meet our criterion of successful count estimation. Trials were continued with $m = 10, 12, 14, 16$. In each case, the value of q appeared to be greater than 0.10. At $m = 18$, 15 drawings gave no failures, from which $q = 0.00$. A sample size of 18 may then possibly be within the desired range. However, with only 15 trials, the 90% limits for q are 0 and 0.24. To be sure that q has a 90% probability of being lower than 0.10, it was necessary to continue sampling. We therefore drew an additional 7 samples of $m = 18$ each. In this set we obtained one failure, giving an estimate of $q = 0.045$ with 90% limits of 0 and 0.17. Sampling was then continued for a total of 66 trys, resulting in 6 failures. The estimate of q

TABLE III-B. Determination of number of basket samples from Tow 33 which must be counted to estimate the total number of fish caught to within 10% of the true total in at least 90% of cases.

No. of baskets in sample for count "m"	Possible No. of different samples	No. of trials "A"	No. of failures "B"	q (= B/A)	90% binomial limits for q
1	33	33	23	0.70	
8	1.4×10^7	15	6	0.40	0.23–1.00
10	9.3×10^7	15	5	0.33	0.17–1.00
12	3.5×10^8	15	6	0.40	0.23–1.00
14	8.2×10^8	15	3	0.20	0–0.40
16	1.2×10^9	15	2	0.13	0–0.32
18	1.0×10^9	15	0	0	0–0.24
18	same	22	1	0.045	0–0.17
18	same	38	4	0.105	0–0.20
18	same	66	6	0.091	0–0.15
19	8.2×10^8	15	3	0.20	0–0.39
19	same	40	5	0.125	0–0.22
20	5.7×10^8	30	0	0	0–0.07

therefore became 0.091 with limits 0 and 0.15. This series indicates that a sample size of 18 baskets must yield a q close to 0.10; however an impractically large number of samples would have to be drawn to establish whether its 90% limits are actually below or above 0.10. Our further trials were therefore continued using 19 baskets per sample rather than 18. At $m = 19$, the first 15 trials yielded 3 failures and a continuation to 40 trials yielded a total of 5 failures from which $q = 0.125$. At this point the sampling with $m = 19$ was discontinued.

At $m = 20$, the counts in a series of 22 trials all fell within the specified 10% limits, yielding an estimate of $q = 0.00$ with 90% limits between 0 and 0.099. A further 8 trials gave no failures and reduced the confidence interval to 0–0.074.

We may conclude that in Tow 33 twenty baskets out of 33 would have given a mean count within 10% of the true count at least in 90% of the cases, the latter statement being verified with probability somewhat better than 0.90.

Similar sets of trial calculations were performed on several other catches. In one of these, Tow 42, a total of 30 baskets was taken, but the assortment of fish from the deck pen into baskets was far less uniform than in the above example; the χ^2 for length distributions among basket-sample units was 154.5 with 18 degrees of freedom. In this case it was found necessary to count 25 out of the 30 baskets to achieve the desired accuracy. However, a major share of the heterogeneity in the counts and size compositions was contributed by 3 baskets which contained mostly small fish. When these 3 baskets were removed from the series, the average count per basket for the remainder fell within the required 10% limits in more than 90% of cases, for a sample size of only 12 baskets out of the 27. If this stratification by size-groups had been done in the field operation, the desired accuracy could then have been achieved by counting only 12 baskets of the larger-sized fish and the 3 baskets of the smaller, rather than 25 baskets from the unstratified "population" of baskets.

The influence of the heterogeneity among sample units on the required level of sampling may be further illustrated by a comparison of the basket with box samples. The 30 baskets from Tow 42 were distributed among 8 boxes, reducing the χ^2 for length compositions to 23.0 with 10 degrees of freedom. In this case it was found that counting the numbers of fish in only 4 out of 8 boxes gave estimates of total count with acceptable accuracy.

It is evident that the efficacy of the sampling for counts depends critically on the sampling design. Stratification, mixing, or some similar procedure which ensures low heterogeneity among sampling units results in appreciable savings in the amount of sampling necessary to achieve a given level of accuracy.

CONCLUSIONS

In general it appears that the basket-lot technique of handling individual species of fish is not a satisfactory procedure on which to base a sampling program. Heterogeneity among the baskets is so great that random sampling for lengths is impossible, and sampling for counts generally requires handling of a high proportion of the catch. The remedy of mixing basket lots and using these as sampling units complicates the deck procedure somewhat, but makes it possible to draw random samples without individual selection of fish from each sampling unit. Under such circumstances, it appears that samples of 200 to 300 fish are large enough to give estimates of relative length compositions within limits acceptable for most purposes. Mixing also permits a reduction in the number of units which must be counted for acceptably accurate estimates of total count.

It appears, however, that the mixing procedure is not effective without some additional stratification of the catch, such as is represented on most research vessels by a species sort. The combined procedure of species sorting and mixing of the initial sampling units can be avoided only by measuring most of the fish or by adopting a closer approach to the ideal scheme in which individual fish are picked randomly (or perhaps systematically) from the catch with fixed sampling ratios. To be expedient the latter method would probably necessitate a mechanical sampling device on board the research vessel.

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Geographic Variation in North American Ninespine Sticklebacks, *Pungitius pungitius*[1]

By J. D. McPhail[2]

Institute of Fisheries, Department of Zoology
University of British Columbia, Vancouver, B.C.

ABSTRACT

Ventral spine length and the number of lateral plates, dorsal spines, and gill rakers in *Pungitius pungitius* from 132 North American localities were compared. The number of lateral plates is consistently high in populations from tidal waters, and low in inland populations. Geographic variation in the number of dorsal spines and gill rakers suggest two allopatric forms of *P. pungitius* in North America. A Bering form ranges from Alaska along the arctic coasts of Canada, and a Mississippi form ranges from the Great Lakes to the Mackenzie River. Two glacial refugia are hypothesised to explain the origin and present distribution of these forms.

INTRODUCTION

The ninespine stickleback, *Pungitius pungitius* (Linnaeus), is widely distributed in lowland areas throughout the northern hemisphere. In North America *Pungitius* ranges from the Aleutian Islands to Newfoundland, and from northern Baffin Island to the Great Lakes (Fig. 6). On the Atlantic coast *Pungitius* is distributed south to New Jersey (Fowler, 1906).

Like many northern freshwater fishes, *Pungitius* is morphologically variable. The geographic patterns of this variation and their interpretation are the theme of the present study.

Several authors have commented on geographic variation in North American *Pungitius*. Bean (1879) in describing a new subspecies, *Gasterosteus pungitius brachypoda*, from Cumberland Sound, Baffin Island, noted that the ventral spines were shorter than those of some southern populations. From this observation Bean postulated a north–south cline in the ventral spine length of *Pungitius*.

Vladykov (1934) and Walters (1955) examined geographic variation in the dorsal spine number of *Pungitius*. Both authors concluded that there is a north–south cline in spine number. Vladykov considered this cline phenotypic, and suggested that the high spine number is environmentally induced. Walters suggested that the cline is due to the environment selectively eliminating individuals with a non-adaptive spine count. This suggestion is based on skewed frequency distributions for dorsal spine number in some of the populations Walters examined.

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[1] Received for publication July 16, 1962.

[2] Author's present address: Department of Zoology, McGill University, Montreal, Quebec.

J. Fish. Res. Bd. Canada, **20**(1), 1963.
Printed in Canada.

The following study presents a re-examination of geographic variation in North American *P. pungitius*, and offers a possible explanation for this variation.

MATERIALS AND METHODS

Over 2500 specimens of *Pungitius pungitius* were examined from 132 localities over the entire North American range of the species. Individuals ranged from 20–70 mm in standard length. Collections were from both inland and tidal waters. The specimens are now in the museums of the Institute of Fisheries of the University of British Columbia, the National Museum of Canada, the Royal Ontario Museum, and the Museum of Zoology at the University of Michigan. The museum number, locality, and summarized data for each collection are presented in an Appendix.

All counts and measurements follow Hubbs and Lagler (1958) except where otherwise noted. The characters selected to illustrate geographic variation in *P. pungitius* are: the number of lateral plates, the length of the ventral spines, the number of dorsal spines, and the number of gill rakers.

The lateral plates were best counted by staining the specimens with alizarin. However, much of the material was borrowed from other institutions and could not be stained. In such cases the lateral plates were counted by passing a fine needle along the lateral line. The two methods of counting were compared and found to give similar results. In specimens with a single, small lateral plate this was occasionally missed using the needle method. In specimens with more than one lateral plate the two methods gave identical results.

Only collections containing ten or more specimens are used in comparisons. Sex ratio and average length showed considerable variation between collections. Because of this variation it is necessary to demonstrate that the characteristics used do not show sexual dimorphism and are not correlated with length. The significance of correlations were tested using the correlation coefficient (Snedecor, 1956). All probability values are at the 5% level of significance.

The number of lateral plates, ventral spine length, number of dorsal spines, and number of gill rakers are not significantly correlated with standard length ($P > 0.1$). Table I illustrates that there is no significant difference between male and female *P. pungitius* in the same characters.

TABLE I. A comparison of lateral plates, ventral spine ratio, dorsal spine number, and gill raker number in male and female *P. pungitius* (30 specimens of each sex). In all cases the probability is nonsignificant ($P > 0.1$).

	Males		Females	
	Range	Mean	Range	Mean
Lateral plates	1–6	3.8	1–6	3.8
Ventral spine ratio	1.5–2.2	1.7	1.4–2.1	1.7
Dorsal spine number	9–11	10.3	9–11	10.5
Gill raker number	10–14	11.6	10–13	12.0

PATTERNS OF GEOGRAPHIC VARIATION

LATERAL PLATES

The lateral plates are small ossified areas along the anterior portion of the lateral line. The number of lateral plates ranged from 0–15 in the populations examined. In some individuals from the Atlantic coast the lateral plates were continuous with the plates forming the caudal keel. Such individuals were rare, and are not included in the above range.

Figure 1 illustrates geographic variation in the number of lateral plates in North American *P. pungitius*. Modal plate counts are used for comparisons because the distribution of plate counts in freshwater populations is not normal. *Pungitius* from tidal areas have well developed lateral plates (modes range from 3 to 5, usually 4). Populations from freshwaters have no lateral plates, or a few, weakly developed plates (modes range from 0 to 2, usually 0). There is no evidence of a north–south cline in plate number.

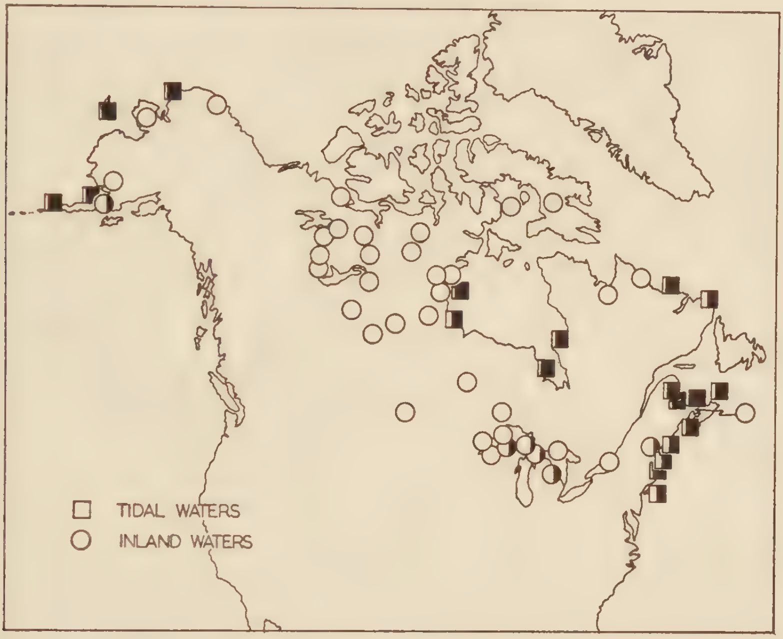

FIG. 1. Variation in the modal number of lateral plates. Solid white symbols indicate a modal plate number of O, solid black symbols a modal plate number of 5. Intermediate populations are represented by symbols in which the amount of black is proportional to the modal plate count.

Heuts (1947) demonstrated the existence of two genotypically distinct races of *Gasterosteus aculeatus* in Europe. One race inhabits marine and brackish water, the other inhabits freshwater. The major morphological difference between these races of *Gasterosteus* is the number of lateral plates. A comparable phenomenon has never been demonstrated in *Pungitius*. However, the data presented in Fig. 1 demonstrate a consistent difference in the number of lateral plates between tidal and freshwater populations of *P. pungitius*. The data of Bertin (1925) show the same difference. Whether this difference is genotypic or phenotypic cannot be determined from the present data.

VENTRAL SPINE LENGTH

In the present study ventral spine length is expressed as a proportion of pectoral fin length. Measurements should not be converted to proportions without making some allowance for allometric growth. In the present case the value obtained by expressing ventral spine length as a proportion of pectoral fin length is not significantly correlated with standard length ($P > 0.1$), and therefore the use of this proportion is valid.

Figure 2 illustrates geographic variation in the length of the ventral spines.

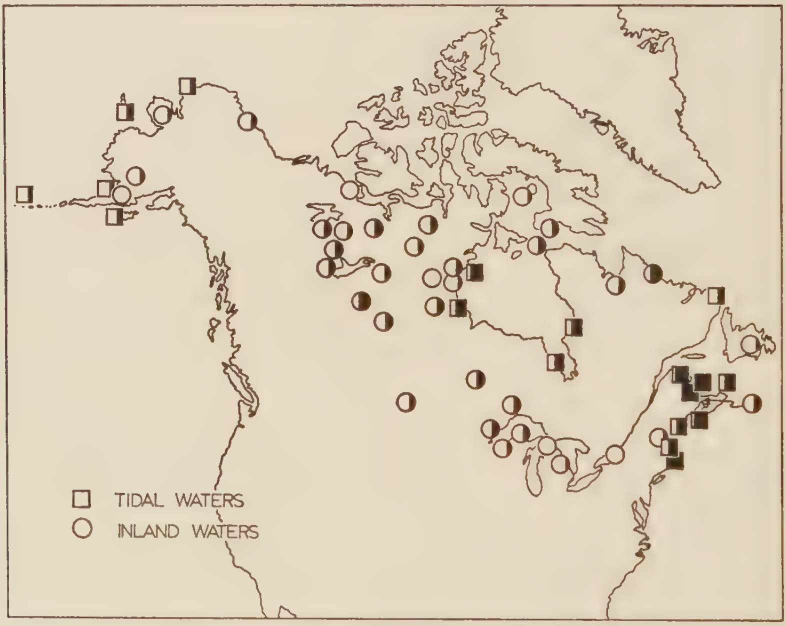

FIG. 2. Variation in mean ventral spine length. The shortest observed ventral spine lengths (pectoral fin to ventral spine ratio of 2.0) are represented by solid white symbols, and the longest ventral spines (ratio of 1.0) by solid black symbols. Intermediate populations are represented by symbols in which the ratio of black to white is proportional to the mean pectoral fin to ventral spine ratio.

Pungitius from tidal areas in the southeastern section of its North American range have the longest ventral spines. Inland populations at the same latitude have much shorter spines. At the northern end of its North American range both tidal and inland *Pungitius* have short ventral spines. There is no indication of a north–south cline in the ventral spine length of inland populations. *Pungitius* from the Great Lakes area have approximately the same ventral spine length as *Pungitius* from Alaska and the Northwest Territories. However, there is a tendency among tidal populations toward longer ventral spines in southern areas. This suggests a north–south cline in ventral spine length in tidal populations. This cline may be environmentally induced. If so, the absence of such cline in inland populations suggests that a combination of temperature and salinity are necessary to produce this effect.

NUMBER OF DORSAL SPINES

The number of dorsal spines varied from 7–12 in the specimens examined. As indicated earlier, Vladykov (1934) and Walters (1955) concluded that there is a north–south cline in the number of dorsal spines.

Figure 3 illustrates geographic variation in dorsal spine number over the North American range of *Pungitius*. The distribution of black symbols and white symbols does not suggest a north–south cline in dorsal spine number. The transition from the area of high mean spine number to the area of low mean spine number is often abrupt. In Fig. 3 the lowest mean spine counts among the populations represented by black symbols are not necessarily found in areas nearest white symbols, but are scattered throughout the area occupied by black symbols. The same is true among the populations represented by white symbols.

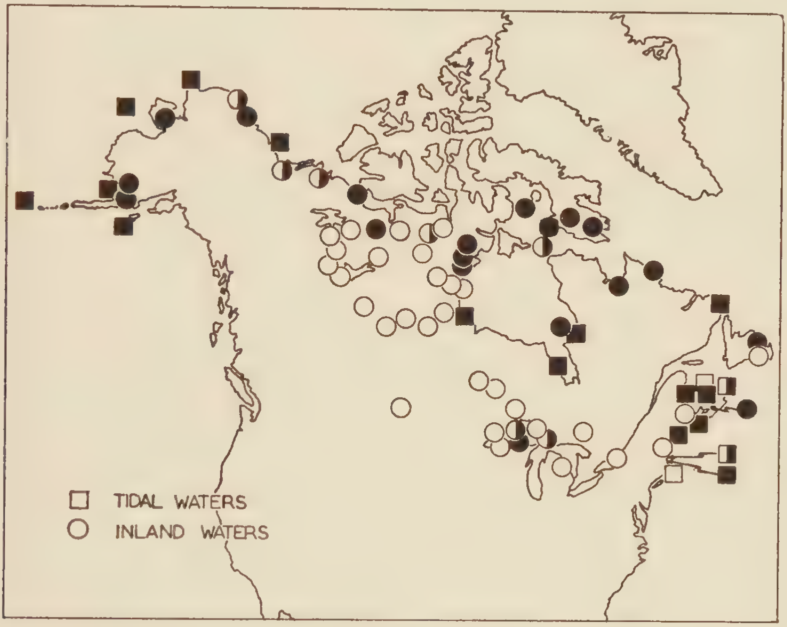

FIG. 3. Variation in mean dorsal spine number. Black symbols indicate populations with mean dorsal spine numbers ranging from 9.7 to 10.7, black and white symbols 9.5 to 9.6, and white symbols 8.7 to 9.4.

Pungitius with high spine counts are distributed from Alaska across arctic Canada, and down the Atlantic coast to the New England states. *Pungitius* with low spine counts are found in the Great Lakes area and northwards across the Great Plains to the Mackenzie Valley. Some of the more northern low spine count populations are found in tundra areas. Populations with intermediate spine counts are found in two main areas: in the Great Lakes, and in the Maritime Provinces and New England states.

The distribution of high spine count and low spine count populations form a distinct pattern. However, there are anomalous populations. Sticklebacks from Gratiot Lake on the Keweenaw Peninsula, Michigan, have a high mean spine count (10.1) in an area characterized by intermediate or low mean spine counts. A collection from the St. Mary's area in Newfoundland has a low mean spine count (8.7) in an area characterized by high mean spine counts. Collections from Branch River and Davis Stream, Maine, and Woods Hole, Massachusetts, have low mean spine counts (8.9, 9.1, and 9.3) in areas characterized by intermediate or high mean spine counts. Aside from these anomalous populations there is considerable uniformity in mean dorsal spine number over wide geographic and climatic areas.

Lindsey (1963) demonstrates that the number of dorsal spines in *Pungitius pungitius* can be modified by the environment. It is suggested that the anomalous spine counts found in some populations may be due to environmental effects, but that the over-all pattern of variation in mean dorsal spine count is not attributable to the environment. A possible explanation for this pattern of variation is presented in the discussion.

Number of Gill Rakers

None of the previous studies on geographic variation in *P. pungitius* used gill rakers. In the populations examined the number of gill rakers on the first arch varied from 10 to 15. Figure 4 shows geographic variation in gill raker number over the North American range of *Pungitius*. The distribution of low gill raker and high gill raker populations show no evidence of a cline. The transition from areas of low mean gill raker count to areas of high mean gill raker count is often abrupt. The highest mean gill raker counts among the populations represented by black symbols are not necessarily found in areas nearest white symbols, but are scattered throughout the area occupied by black symbols. The same is true among the populations represented by white symbols.

The geographic distribution of low gill raker and high gill raker populations form a pattern almost identical to that in Fig. 3. The major differences are in the Great Lakes area and the Atlantic coast. These areas are characterized by a high proportion of populations with intermediate mean dorsal spine counts. However, the mean gill raker counts are not intermediate. Great Lakes *Pungitius* have consistently high gill raker counts, while Atlantic coast *Pungitius* have consistently low gill raker counts. Also, the populations with anomalous spine counts (Fig. 3) have normal gill raker counts for their area (Fig. 4). This evidence suggests that the number of gill rakers is less subject to variation than the number of dorsal spines.

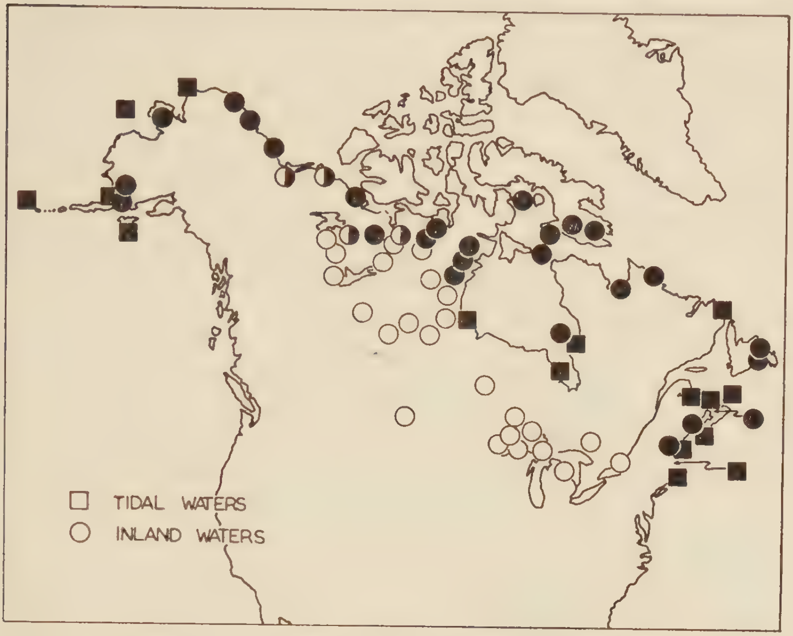

FIG. 4. Variation in mean gill raker number. Black symbols indicate populations with mean gill raker numbers ranging from 10.8 to 12.5, black and white symbols 12.6 to 12.7, and white symbols 12.8 to 13.6.

DISCUSSION

Figures 3 and 4 indicate the presence of two morphological forms of *P. ungitius* in North America. These forms are allopatric and display considerable orphological uniformity over wide geographic and climatic areas. It is therere suggested that the differences between the two North American forms of . *pungitius* have a genetic basis. The two forms apparently intergrade wherever ey come in contact.

The existence of two genetically differentiated forms of *P. pungitius* in orth America can be explained by hypothesizing the isolation of this species two widely separated glacial refugia. Because the amount of morphological fferentiation is slight it might be assumed that this differentiation is largely result of the Wisconsin glaciation. However, this assumption may not be tirely warranted. The genus *Pungitius* is conservative. David (1945) scribed a fossil species (*Pungitius haynesi*) from the Pliocene or upper Miocene California. The counts and proportions of this Neogene stickleback are within e range of living *P. pungitius*. The genus has scarcely differentiated since the iocene; therefore, the differences between the North American forms of *P. ngitius* may reflect pre-Wisconsin as well as Wisconsin isolation. The present stribution of the two forms is mainly a result of postglacial dispersal.

Several authors discuss possible glacial refugia and postglacial dispersal utes for *P. pungitius*. Radforth (1944) suggests that *Pungitius* survived in the unglaciated regions of Alaska, and dispersed to the southeast from this refugium. This suggestion is based on details of the present distribution, in particular the absence of *Pungitius* from the upper Mississippi drainages.

Walters (1955) postulates two glacial refugia for North American *P. pungitius*: the Bering refugium (including the arctic slope of Alaska and adjacent parts of Siberia), and the upper Mississippi Valley. Walters suggests that the present distribution of *P. pungitius* was attained when populations dispersing from these refugia met near the arctic coast. Walters' hypothesis is also basec on details of the present distribution, in particular the occurrence of *Pungitius* above the rapids on the Slave River at Fort Smith.

Underhill (1957) postulates the postglacial dispersal of *P. pungitius* (anc several other species) from some eastern North American refugium. Dispersa to the northeast was accomplished through the eastern outlets of Lake Agassiz Underhill's suggestion is based on the existence of eastern outlets from Lake Agassiz and the absence of *Pungitius* from the upper Mississippi Valley.

The above suggestions are based on circumstantial evidence. Little direct evidence can be obtained regarding the use of one or another refugium by a particular species. The best evidence is accurately dated fossil material, but in the present case no North American Pleistocene fossils are available. The distribution of relict populations in relation to the continuous range of a species may also supply direct evidence concerning glacial refugia. Again, such evidence is not available for *P. pungitius*. Genotypic morphological differentiation can also provide evidence concerning glacial refugia. For such differentiation to occur isolation is necessary. Therefore, the existence of allopatric, morphologically differentiated forms of a species is evidence that the species has been separated into isolated populations. In the present case the two North American forms of *P. pungitius* strongly support Walters' contention that *P. pungitius* survived glaciation in two refugia.

Both Radforth (1944) and Underhill (1957) object to the upper Mississipp Valley as a refugium for *P. pungitius* because the species is now absent from this area. However, the absence of *P. pungitius* from Lake Erie indicates that this species can be eliminated by changing ecological conditions. Therefore, the present absence of *Pungitius* from the upper Mississippi does not preclude this area as a possible refugium for this species.

Underhill (1957) suggests a refugium to the east of the upper Mississipp Valley for *P. pungitius* and a number of other species. No particular area is indicated. For *Pungitius* any eastern refugium, except perhaps the Atlantic Coast, presents the same problem as the upper Mississippi refugium, namely the absence of the species at the present time. Since there is no evidence to sugges an Atlantic Coast refugium for *Pungitius*, it is assumed that the southern refu gium was in the upper Mississippi Valley (including the driftless area o Wisconsin).

Figure 5 shows the hypothetical distribution of the Bering and Mississipp forms of *Pungitius* with the Wisconsin ice-sheets at their maxima. As the ice sheets retreated *Pungitius* dispersed into the newly exposed areas. The presen

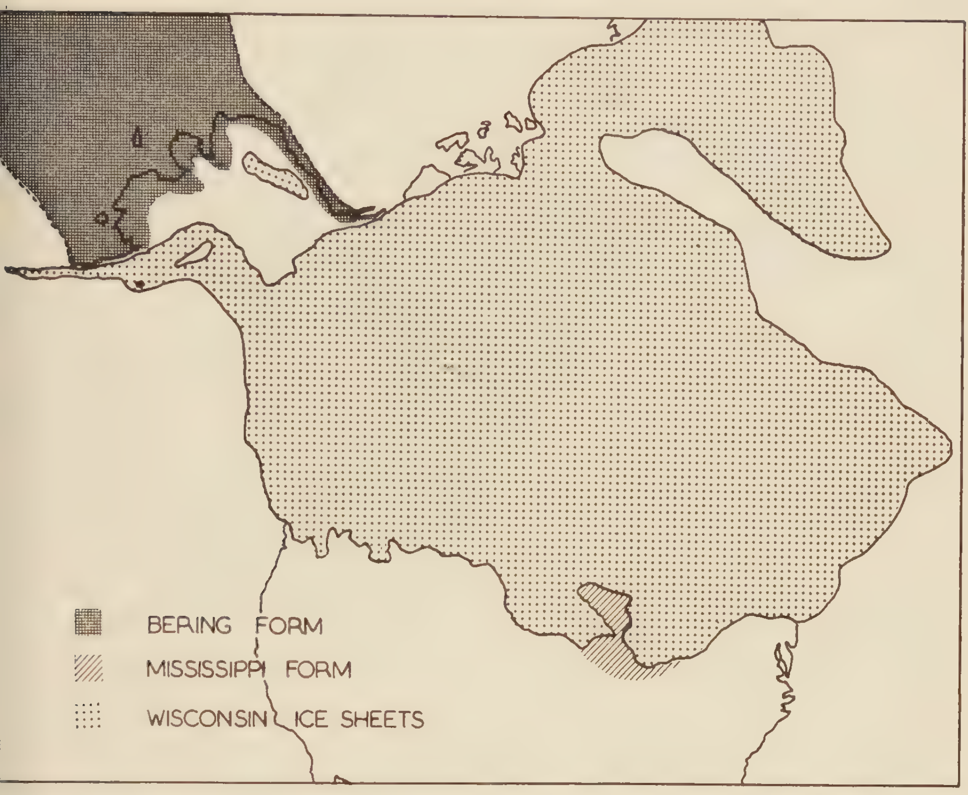

FIG. 5. Hypothetical distribution of the Bering and Mississippi forms of *P. pungitius* during the Wisconsin glaciation. The ice-sheets are shown at their Wisconsin maxima. Glacial boundaries are from Flint (1957), Craig and Fyles (1960), and Karlstrom (1960).

distribution of the Bering and Mississippi forms of *Pungitius pungitius* is largely a result of the pattern of deglaciation of the Wisconsin Laurentide ice-sheet.

The details of deglaciation in the Great Lakes area are summarized by Flint (1957). Elson (1957) discusses deglaciation on the northern Great Plains, and Ives (1960) outlines the deglaciation of Labrador–Ungava. Craig and Fyles (1960) outline Wisconsin deglaciation in the Northwest Territories.

Zoogeographically, the most important point revealed by these researches on deglaciation is that the continental sea coasts became ice free relatively early. This resulted in a continuous sea connection from Alaska along the Arctic coast of Canada and down the Atlantic coast by about 8,000 years ago. At this time parts of the northern Great Lakes Basin, and much of the interior of the Northwest Territories, were still ice covered.

Figure 6 presents the known North American distribution of the Bering form of *P. pungitius*. Dispersal from the Bering refugium was in two directions: to the southwest, and to the southeast. *Pungitius* dispersed to the southwest along the Aleutian Islands and around the Alaska Peninsula to Kodiak Island and Cook Inlet. It is possible that the Kodiak Island and Cook Inlet populations

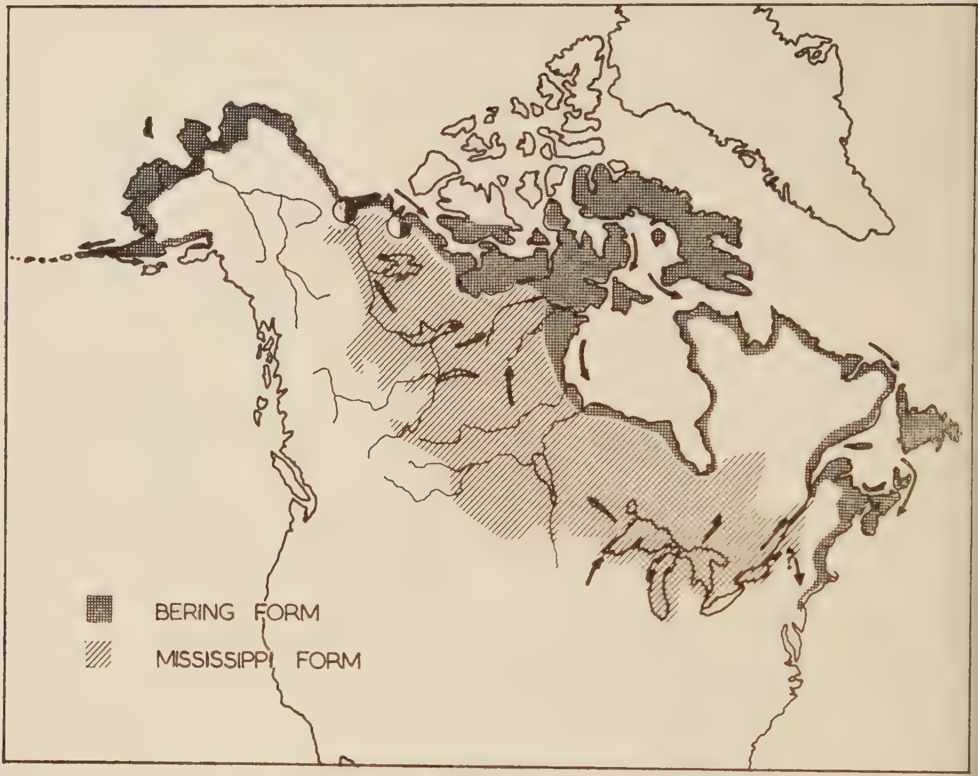

FIG. 6. The present distribution of the Bering and Mississippi forms of *P. pungitius*. The arrows indicate possible postglacial dispersal routes. The black and white circles indicate areas where intermediate populations are known to occur.

survived in these areas. Karlstrom (1960) presents data which suggest that parts of Kodiak Island (Karluk Lake area) and Cook Inlet were unglaciated during the Wisconsin. It is not known whether Karluk Lake *Pungitius* are morphologically differentiated from other Alaskan *Pungitius*. Cook Inlet *Pungitius* are not.

The dispersal of Bering *Pungitius* to the southeast was more extensive Along the arctic coast the Laurentide ice-sheet retreated to the southeast (Craig and Fyles, 1960). *Pungitius* probably followed the ice-sheet closely. By 10,000 years ago the arctic coast was ice free almost to Coronation Gulf (Craig, 1960). The Gulf of Boothia area became ice free about 8000 years ago (Craig, 1961). The sea entered Hudson Bay and Foxe Basin 7000 to 8000 years ago (Lee, 1960). Bering *Pungitius* were then able to disperse into Hudson Bay and down the Atlantic coast. Bering *Pungitius* have also reached the southern islands of the Arctic Archipelago (recorded from Victoria, King William, and Baffin Islands), and all of the islands of Hudson Bay.

Figure 6 also presents the known distribution of the Mississippi form of *P. pungitius*. Mississippi *Pungitius* probably survived the Wisconsin glaciation n the upper Mississippi Valley. From here *Pungitius* spread northwards into the glacial Great Lakes, probably through the St. Croix outlet of Lake Duluth. The early presence of *Pungitius* in Lake Duluth is suggested by its occurrence n Lake Desor, Isle Royale, and lakes in the Porcupine Mountains. (Hubbs and Lagler, 1949). From Lake Duluth *Pungitius* dispersed in two directions: to the east, and to the northwest.

Pungitius spread to the east through the late glacial Great Lakes, and probably from there into the St. Lawrence Valley. It is not known which form of *Pungitius* occupies the lower St. Lawrence Valley. The valley was flooded postglacially by the Champlain Sea. Recent studies (Terasmae, 1959) date the Champlain Sea at 11,000 to 10,000 years ago. This means that the valley had emerged (about 9000 years ago (Terasmae, 1959)) before Bering *Pungitius* reached the Atlantic coast. The populations of *Pungitius* in the upper St. Lawrence Valley are the Mississippi form.

Mississippi *Pungitius* occur in the upper portions of many rivers entering James Bay and southwestern Hudson Bay. They probably reached this area by headwater captures, or through Lake Barlow-Ojibway.

The dispersal of Mississippi *Pungitius* to the northwest has been extensive. From Lake Duluth *Pungitius* probably spread into Lake Agassiz II through one of the eastern outlets. From Lake Agassiz II, *Pungitius* dispersed throughout the northern Great Plains. At one stage in deglaciation Great Bear Lake and Great Slave Lake formed a continuous lake (Craig, 1961). This glacial lake lowed southwards through the Slave River Valley. Mississippi *Pungitius* probably entered the Mackenzie system through this connection. Later the present outlet of Great Bear Lake came into use, and Mississippi *Pungitius* could hen disperse downstream towards the delta. The presence of Mississippi *Pungitius* in the upper portion of the Coppermine River (Redrock Lake) is probably due to headwater capture from the Mackenzie River. The headwaters of these rivers interdigitate in low tundra areas.

Barton and Broscoe (1961) report the capture of a Mackenzie tributary by the Anderson River. The presence of Mississippi *P. pungitius* and *Couesius plumbeus* in the Anderson River are probably explained in this way. Mississippi *Pungitius* also occur in the Thelon, Dubawnt, and Kazan Rivers. The presence of *Couesius plumbeus* and *Cottus ricei* in the Thelon, *Catostomus comersonii* and *Couesius plumbeus* in the Dubawnt, and *Couesius plumbeus* in the Kazan indicate hat these rivers have received part of their fish fauna from the south. *Pungitius* probably entered the Thelon from the Mackenzie River, and the Dubawnt and Kazan from the Churchill River.

Figure 6 indicates that dispersal from the Bering refugium was mainly hrough coastal waters, while dispersal from the Mississippi refugium was through reshwater. A possible explanation for this difference in dispersal routes may e obtained by considering the refugia. During the Wisconsin *Pungitius* urviving in the Bering refugium were in constant contact with the sea. These opulations retained the ability to disperse through seawater. In contrast, the

Pungitius surviving in the Mississippi refugium were isolated from the sea, and may have partially lost the ability to disperse through seawater.

The collections from Aklavik, on the Mackenzie Delta, and the Anderson River are intermediate in both mean dorsal spine number and mean gill raker number. Both populations are from areas where Bering and Mississippi *Pungitius* come in contact, and probably represent intergrades in the sense of Gilbert (1961).

A collection from the Back River (MacDougall Lake) has a mean spine number of 9.3 (Mississippi form) and a mean gill raker number of 11.5 (Bering form). *Pungitius* from the nearby headwaters of the Ellice River have a mean spine number of 9.2 and a mean gill raker number of 12.6 (intermediate). Tributaries of the Back River rise close to tributaries of the Mackenzie and Thelon Rivers (both containing Mississippi *Pungitius*). The Back and Ellice River populations probably represent partial intergrades between the Mississippi and Bering forms of *Pungitius*.

Other areas of intergradation probably exist, particularly along the southwestern shores of Hudson and James Bays, and the lower St. Lawrence Valley. Judging from mean gill raker counts, Atlantic Coast *Pungitius* (from the Gulf of St. Lawrence to New Jersey) are predominately the Bering form. However, within this area there is wider variation in mean dorsal spine number than in any other area (Fig. 3). This may be due to gene exchange with the Mississippi form through the lower St. Lawrence Valley, or perhaps during glacial time, through the Hudson Valley outlets of the glacial Great Lakes.

TAXONOMIC STATUS OF THE NORTH AMERICAN FORMS OF *PUNGITIUS PUNGITIUS*

Most ichthyologists agree that a species is properly divisible into subspecies when it is established that the species consists of two or more allopatric, genetically differentiated forms separated by a relatively narrow zone of intergradation. Evidence presented in the preceding study indicates the existence of two allopatric, morphologically differentiated forms of *Pungitius* in North America. Apparently these forms intergrade when they come in contact. The evidence suggests that the differences between these forms are genotypic.

In these respects the two North American forms of *Pungitius pungitius* answer the requirements of subspecies. However, the degree of differentiation is slight. Over 90% of the North American *populations* can be distinguished using mean gill raker count, but in a sample of 1000 taken randomly from both forms only 18% of the *individuals* could be distinguished by gill raker count.

Hubbs (1943) suggests that much more than half of a given population should be distinguishable in order to warrant subspecific recognition. Bailey, Winn and Smith (1954) suggest that at least 93% of the individuals should be distinguishable. It is the opinion of the writer that the degree of differentiation between the two North American forms of *Pungitius pungitius* is not sufficient to warrant subspecific recognition.

ACKNOWLEDGMENTS

Financial support for this study was provided by the Arctic Institute of orth America and the University of British Columbia. Most of the material om the Northwest Territories was collected by the Fisheries Research Board of anada Arctic Unit, on the 1959 Barren Grounds Survey. Drs C. C. Lindsey nd N. J. Wilimovsky read the manuscript. Their criticisms and suggestions re gratefully acknowledged. Drs W. B. Scott and E. J. Crossman, Royal ntario Museum, and Mr D. E. McAllister, National Museum of Canada, indly loaned specimens. The author also wishes to thank Drs R. M. Bailey, V. B. Scott and E. J. Crossman for kindness and courtesy during visits to the niversity of Michigan Museum of Zoology, and the Royal Ontario Museum. wish particularly to thank Dr Crossman for his aid.

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APPENDIX

Data pertaining to specimens of *Pungitius pungitius* examined in this study. Abbreviations for museums are: B.C., University of British Columbia; UM, University of Michigan; NMC National Museum of Canada; ROM, Royal Ontario Museum. Collections without museum numbers represent uncataloged material at McGill University and the University of British Columbia. Latitudes and Longitudes are approximate. Collections from tidal areas are marked by a +, inland collections by a –.

Museum No.	Locality	Approx.		No. of specimens examined	Tidal influence	Lateral plates		Dorsal spines		Pectoral fin to ventral spine ratio		Gill rakers	
		Lat. N.	Long. W.			Range	Mode	Range	Mean	Range	Mean	Range	Mean
ALASKA:													
	Meade River	70°28′	157°20′	30	–	0–1	0	8–11	9.8	1.5–2.3	1.7	10–13	12.0
BC58-199	Turnagain Arm	61°07′	150°03′	4	+	3–4	4	9–10	9.5	1.5–1.8	1.6	11–12	11.5
UM106211	Sitkalidak Is.	57°07′	153°10′	30	+	...	–	9–12	10.7	1.3–2.0	1.7	10–13	11.0
	Attu Is.	52°30′	173°08′	15	+	2–7	4	9–12	10.3	1.6–2.0	1.8	10–13	11.0
BC60-408	Naknek L.	58°50′	156°00′	24	–	1–5	2	9–11	10.1	1.7–2.5	2.0	10–14	12.5
BC60-409	King Salmon Cr.	58°50′	157°05′	30	+	0–6	4	9–11	10.1	1.2–1.8	1.5	10–13	11.9
BC60-455	Snag Pt.	59°02′	158°26′	7	+	3–7	4	10–11	10.7	1.4–7.0	1.6	10–13	11.7
BC60-401	Aleknagik L.	59°12′	158°35′	32	–	0–3	0	10–12	10.5	1.5–1.9	1.8	10–13	11.2
BC60-388	Alakanuk.	62°42′	164°40′	1	+	...	0	...	10.0	...	...	...	12.0
BC60-383	Tomname	63°18′	169°04′	80	+	1–6	4	9–11	10.4	1.4–2.2	1.7	10–14	11.8
BC60-376	Salmon L.	64°50′	165°00′	30	–	0–3	0	10–11	10.4	1.4–2.3	1.9	10–13	11.5
	Singakit R.	68°12′	165°50′	35	+	2–6	4	9–11	10.3	1.6–2.1	1.8	11–13	12.1
	Ikroavik L.	71°02′	156°30′	50	–	0–4	0	8–11	9.6	1.5–2.0	1.7	10–14	11.7
	Half Moon Three	70°45′	155°00′	30	–	...	...	8–11	9.7	1.6–2.0	1.8	11–13	12.3
	Itkillik R.	70°03′	151°02′	1	–	0	0	10	10.0	...	...	11	11.0
BC60-385	Unalakleet R.	63°52′	160°47′	1	+	0	0	10	10.0	...	...	12	12.0
BC58-567	Colville R.	70°40′	150°30′	2	–	...	...	9–10	9.5	...	...	11	11.0
BC58-577	Lake near Kikiakroak R.	69°58′	151°50′	6	–	0	0	9–11	10.0	...	...	10–12	11.1
Y.T:													
	Herschel Is.	69°35′	139°05′	30	+	...	...	9–11	10.0	...	...	11–14	12.5
DIST. OF MACKENZIE:													
	Horton R.	70°02′	126°40′	30	+	...	...	9–11	9.8	...	...	10–13	12.1
	Aklavik	68°12′	135°00′	35	–	...	...	8–10	9.6	...	...	10–13	12.6
	Anderson R.	69°43′	128°58′	32	+	...	...	9–11	9.6	...	...	11–14	12.7
NMC58-72	Bernard Hb.	68°45′	114°45′	48	–	0–4	0	8–11	9.8	1.6–2.5	2.0	10–14	11.9
BC60-38	Beaverlodge L.	64°42′	118°12′	40	+	0–2	0	8–10	8.8	1.3–2.0	1.6	12–17	13.3
BC60-303	Lac La Martre	63°15′	116°55′	45	–	0–3	0	8–10	9.0	1.2–1.9	1.6	12–15	13.2
BC61-52	Redrock L.	65°28′	115°02′	60	–	0–4	0	8–10	8.9	1.4–2.2	1.8	12–14	12.7
BC61-333	Trib. to Birch L.	62°04′	116°33′	12	–	0–5	0	7–10	8.8	1.4–2.0	1.7	12–15	13.3
BC61-332	Stagg R.	62°34′	115°44′	17	–	0–2	0	9–10	9.4	1.0–1.6	1.2	12–13	12.9
BC61-325	Kakisa L.	60°55′	117°40′	5	–	0	0	9–10	9.3	...	...	...	...
BC61-42	Dismal L.	67°26′	117°07′	6	–	0–3	0	8–10	9.2	...	...	...	...
BC60-96	Whitefish L.	62°41′	106°48′	5	–	0–1	0	7–9	8.2	1.6–2.1	1.8	13–15	13.6
BC60-100	Wholdaia L.	60°43′	104°10′	1	–	...	0	...	9.0	...	...	14	14.0
BC60-90	Vaillant L.	66°13′	114°30′	8	–	0–3	0	8–9	8.8	...	...	12–14	13.0
BC60-49	Beechy L.	65°25′	106°50′	7	–	0–7	0	8–10	9.0	...	...	11–12	12.5
BC60-81	Kathawachaga L.	66°14′	110°43′	70	–	0–2	0	9–11	9.9	1.3–1.9	1.6	10–13	11.5
BC60-71	Ellice L.	66°00′	106°20′	19	–	0–2	0	8–10	9.2	...	...	11–14	12.6
BC60-60	Clinton Colden L.	64°58′	107°27′	30	–	0–3	0	8–11	9.1	1.5–2.2	1.8	11–14	13.1
BC60-89	Starvation L.	64°54′	112°45′	4	–	...	...	8–9	8.9	...	..	12–14	13.0

Museum No.	Locality	Approx.		No. of specimens examined	Tidal influence	Lateral plates		Dorsal spines		Pectoral fin to ventral spine ratio		Gill rakers	
		Lat. N.	Long. W.			Range	Mode	Range	Mean	Range	Mean	Range	Mean
DIST. OF KEEWATIN:													
BC60-88	MacDougall L.	65°58′	98°37′	40	–	0–3	0	8–10	9.1	1.3–2.0	1.7	10–13	11.4
BC61-50	MacDougall L.	65°58′	98°37′	35	–	0–4	0	8–11	9.5	1.3–2.2	1.6	10–13	11.5
BC60-57	Beverley L.	64°36′	100°30′	53	–	0–2	0	8–10	9.3	1.5–2.2	1.8	11–14	12.9
BC60-64	Dubwant L.	63°08′	101°30′	2	–	0	0	8–9	8.5	...	...	12–13	12.5
BC60-42	Angikuni L.	62°13′	99°50′	21	–	0–2	0	8–10	9.2	1.8–2.5	2.0	12–14	13.1
BC60-35+37	Maguse L.	61°40′	95°10′	12	–	0–1	0	9–11	9.7	...	...	11–13	12.2
BC61-51	Maze L.	62°23′	93°30′	30	–	0–2	0	9–11	10.1	1.5–2.2	1.7	11–12	11.5
BC61-39	Hyde L.	60°35′	95°15′	10	–	0–3	0	8–9	9.0	1.7–2.1	1.9	12–14	13.1
BC61-41	Armit L.	64°10′	91°32′	11	–	0–4	0	9–11	10.1	...	...	11–14	12.0
BC61-36	Meliadine L.	63°05′	92°25′	37	–	0–2	0	9–11	9.8	1.5–2.0	1.8	10–14	11.4
NMC59-57	Eskimo Pt.	58°47′	94°14′	6	+	0–5	4	9–10	9.8	1.1–1.6	1.3	11–13	12.0
DIST. OF FRANKLIN:													
BC61-359	Cambridge Bay	69°03′	105°05′	2	+	...	...	10	10.0	...	...	11	11.0
	Sapuladjuk	64°11′	76°29′	31	–	...	...	9–11	9.9	1.4–2.0	1.7	10–13	11.7
NMC58-256	Nettilling L.	66°30′	70°40′	9	–	0–3	0	8–11	10.0	1.6–2.2	1.9	11–13	11.8
	Shona L.	63°44′	68°28′	27	–	0–2	0	9–12	10.1	...	...	10–13	11.4
ROM18598	Akimiski Is.	53°00′	81°20′	10	+	0–5	4	9–11	10.0	1.1–1.8	1.4	11–13	12.2
NMC60-109	Rowley Is.	69°08′	77°15′	24	–	0–1	0	9–11	9.8	1.7–2.3	1.9	11–13	11.8
ROM14140	Nottingham Is.	63°06′	78°00′	25	?	...	...	8–10	9.6	1.4–2.1	1.6	10–13	11.5
LABRADOR–QUEBEC:													
BC62-182	Gt. Whale R.	55°25′	77°50′	22	+	1–5	4	8–11	9.7	1.3–1.9	1.5	10–14	12.2
	Richmond Gulf	56°20′	76°20′	9	+	...	...	9–11	10.0	...	...	12–13	12.4
NMC59-471	Ungava Bay	57°45′	67°30′	35	–	...	...	9–12	10.1	1.4–1.9	1.7	11–14	12.5
BC62-138	Nain	56°30′	61°50′	24	–	0–5	0	9–12	10.0	1.2–1.6	1.4	10–13	12.0
UM160737	Gt. Caribou Is.			30	+	1–4	3	9–11	10.3	1.5–1.9	1.7	10–13	11.4
	Belcher Is.	56°32′	79°00′	30	–	...	...	8–11	9.8	...	...	10–14	12.5
UM160740	Battle Hb.	52°30′	56°40′	10	+	0–4	3	9–11	10.0	1.3–2.0	1.6	10–13	11.0
NMC59-262	Riviere des Rosiers	48°00′	70°00′	2	–	...	...	9–10	9.5	...	...	...	...
NMC58-335	Maria	48°14′	66°02′	7	+	3–8	4	9–11	10.0	1.0–1.3	1.2	12–13	12.4
NEWFOUNDLAND:													
ROM20972	St. Marys	47°00′	53°30′	47	–	...	...	8–10	8.7	1.5–2.2	1.9	10–13	11.3
ROM21010	Gambo L.	49°00′	54°20′	37	–	...	...	9–11	9.9	...	...	11–13	11.6
PRINCE EDWARD IS.:													
NMC59-290	Borden	46°10′	63°45′	43	+	2–7	4	8–11	9.7	0.9–1.3	1.0	11–14	12.8
ROM19040	Bideford R.	46°00′	63°00′	46	+	2–14	5	9–10	9.5	0.9–1.1	1.0	11–13	12.3
NMC58-323	Burlington	46°05′	63°10′	10	+	2–6	4	9–10	9.4	1.0–1.3	1.1	11–13	11.5
NOVA SCOTIA:													
NMC58-327	Oxford	45°35′	63°52′	62	–	0–3	0	9–11	9.8	1.3–2.0	1.5	11–13	11.2
NMC59-292	Cariboo R.	45°40′	62°35′	15	+	0–4	3	9–11	9.8	1.2–1.5	1.3	11–13	11.8
NMC59-310	Plymton	44°20′	65°56′	10	+	4–8	4	9–11	10.3	0.9–1.3	1.1	11–14	12.3
ROM17331	Baddek	46°00′	60°50′	10	+	0–5	4	8–10	9.5	1.2–1.9	1.4	11–13	12.1
NMC58-2994	Coldbrook	45°00′	63°30′	30	+	0–6	4	9–11	10.0	1.1–1.6	1.3	11–13	12.0

Museum No.	Locality	Approx.		No. of specimens examined	Tidal influence	Lateral plates		Dorsal spines		Pectoral fin to ventral spine ratio		Gill rakers	
		Lat. N.	Long. W.			Range	Mode	Range	Mean	Range	Mean	Range	Mean
NEW BRUNSWICK:													
ROM16568	Miramichi R.	46°45′	65°50′	50	+	2–15	4	9–11	9.8	0.9–1.2	1.0	10–13	12.0
NMC59317	St. Andrews	44°56′	67°05′	30	–	...	...	8–10	9.1	...	...	11–13	12.0
NMC59-281	Bransfield	47°00′	64°45′	23	+	2–6	4	9–11	10.0	1.0–1.4	1.2	11–13	12.0
MAINE:													
UM63085	Belfast	44°25′	69°05′	2	+	2–8	...	10	10.0	1.1–1.2	1.2	12	12.0
UM65946	Freeport	43°50′	69°56′	11	+	2–5	3	9–11	9.7	1.2–1.7	1.4	10–13	11.4
UM145410	Branch R.	44°35′	69°45′	30	–	0–3	2	8–10	8.9	1.4–2.0	1.8	10–13	11.2
UM145519	Davis St.	44°10′	69°50′	30	–	0–2	0	8–10	9.1	1.2–1.8	1.6	10–14	11.7
UM140609	Porters Landing Cr.	43°50′	69°50′	30	+	2–5	3	8–11	9.5	1.1–1.6	1.3	10–13	11.3
UM129647	Goosefare Brook	43°25′	70°30′	7	?	...	...	10–11	10.5	1.3–1.7	1.5	10–13	12.0
	Grand Lake Stream	45°08′	67°40′	6	–	...	...	9–10	9.5	1.5–2.0	1.7	10–12	11.7
UM127022	Deer Is.	44°10′	68°40′	2	+	3–6	...	9–10	9.5	1.1–1.3	1.2	11	11.0
UM127038	Pierre Paul Brook	44°35′	68°50′	2	–	0–1	...	9–10	9.5	1.7–1.9	1.8	12–13	12.5
NEW HAMPSHIRE:													
UM140527	Hampton Beach	43°00′	70°40′	30	+	1–6	3	9–11	9.5	1.0–1.7	1.5	10–13	11.0
MASSACHUSETTS:													
UM65105	Woods Hole	41°30′	70°45′	10	+	1–5	3	9–10	9.4	1.0–1.2	1.1	10–13	11.3
UM65080	Woods Hole	41°31′	70°45′	10	+	...	...	8–10	9.3	1.1–1.3	1.2	10–13	12.0
UM140520	Saugus R. mouth	42°30′	71°00′	3	+	3–5	3	9–10	9.7	1.1–1.6	1.3	10–12	11.4
UM140536	Point of Pines	42°15′	71°00′	30	+	0–5	4	9–11	10.0	0.9–1.4	1.0	10–13	11.5
UM140648	Lynn Harbour	42°30′	71°00′	30	+	0–7	4	8–11	9.6	0.9–1.3	1.1	10–13	11.3
NEW YORK:													
UM104000	Oyster Pond	41°40′	73°30′	8	+	0–6	3	9–11	9.5	1.0–1.3	1.1	10–13	12.0
ROM1884	Brooklyn	41°50′	73°55′	3	?	...	...	9–10	9.3	...	...	12–13	12.5
ONTARIO:													
ROM20025	Charlie L.	48°00′	79°30′	10	–	0–3	0	9	9.0	...	...	12–15	13.8
ROM4893	Bay of Quinte	44°00′	76°30′	22	–	0–2	0	9–11	9.4	1.6–2.4	2.0	12–14	13.6
UM56551	Lake Nipigon	49°30′	88°10′	30	–	0–3	0	8–10	9.2	1.5–2.0	1.7	11–14	13.0
ROM12248	Attawapiskat L.	52°40′	88°00′	18	–	...	...	8–10	8.9	...	...	...	...
ROM12568	Ft. Severn	56°10′	88°40′	3	+	...	...	11	11.0	1.4–1.6	1.5	...	...
ROM14493	Kesagami L.	50°30′	80°00′	1	–	...	...	10	10.0	...	...	...	...
ROM14151	Albany R.	52°30′	82°10′	1	+	...	...	10	10.0	1.4	1.4	...	...
ROM7713	Moose R.	51°40′	80°40′	7	+	...	...	9–10	9.7	1.1–1.9	1.4	...	...
ROM21342	Sutton L.	54°10′	84°55′	1	–	...	...	8	8.0	...	...	...	...
ROM21257	Big Trout L.	53°45′	90°00′	30	–	0–2	0	8–10	8.9	1.3–1.9	1.6	12–14	13.1
UM56165	Michipicoten Is.	47°50′	85°40′	23	–	0–3	0	9–10	9.2	1.5–2.1	1.9	11–14	12.8
BC58-380	Lake of the Woods	49°10′	95°00′	1	–	0	0	10	10.0	...	...	13	13.0
BC61-20	Deer L.	53°00′	94°00′	8	–	0–2	0	9–10	9.3	...	...	...	...

Museum No.	Locality	Approx.		No. of specimens examined	Tidal influence	Lateral plates		Dorsal spines		Pectoral fin to ventral spine ratio		Gill rakers	
		Lat. N.	Long. W.			Range	Mode	Range	Mean	Range	Mean	Range	Mean
MICHIGAN:													
UM162546	Black R.	43°40′	84°30′	34	–	0–6	2	8–10	9.1	1.6–2.2	1.9	12–15	13.4
UM13301	Gratiot L.	47°00′	88°30′	11	–	0–4	2	10–11	10.1	1.4–1.8	1.7	12–14	12.9
UM126450	Beaver Is.	45°40′	85°30′	7	–	0–3	1	9–10	9.6	1.7–2.4	2.0	11–14	12.8
UM82072	Whitefish Bay	46°30′	84°50′	23	–	0–4	0	9–11	9.5	1.5–2.0	1.8	12–14	12.9
UM81703	L. Superior	46°30′	87°00′	23	–	0–4	1	8–10	9.3	1.7–2.2	1.9	11–14	13.2
UM70044	Keweenan Bay	47°00′	88°00′	30	–	...	...	8–10	9.2	...	...	...	...
UM99974	Isle Royale	48°00′	89°00′	37	–	0–2	0	8–10	9.5	1.5–1.9	1.7	12–14	13.1
WISCONSIN:													
UM80072	Mouth Amnicon R.	46°30′	90°50′	8	–	0–3	0	9–11	9.4	1.6–2.1	1.8	12–14	13.0
MINNESOTA:													
UM56570	Devils Track R.	47°35′	90°55′	51	–	0–4	0	8–10	9.1	1.4–1.9	1.7	11–15	12.9
MANITOBA:													
ROM17523	N. Knife L.	57°20′	97°20′	15	–	0–4	0	9–10	9.4	1.5–1.9	1.7	11–14	13.0
ROM17525	S. Knife L.	58°11′	93°23′	10	–	...	..	9–10	9.1	...	...	12–14	13.1
ROM17535	Etawaney L.	57°49′	96°51′	5	–	...	...	8–10	9.0	...	...	12–13	12.9
ROM17311	Mukatawa R.	53°10′	97°30′	2	–	...	...	9	9.0	1.5–1.7	1.6	12	12.0
ROM17312	Spider Is.	53°25′	97°40′	4	–	...	...	9	9.0	...	...	12–13	12.9
ROM17290	Dumpty L.			31	–	0–3	0	8–10	9.1	1.4–2.0	1.7	12–14	13.2
ROM14798	Eden L.	56°38′	100°15′	28	–	...	...	7–10	9.1	...	...	11–14	13.0
ROM14814	McGavok L.	50°42′	96°58′	10	–	...	...	8–10	9.1	...	...	12–14	13.1
ROM14138	Churchill	58°40′	94°00′	30	+	0–5	3	8–11	9.7	1.2–1.8	1.4	11–14	12.0
SASKATCHEWAN:													
ROM17579	Little Quill L.	57°50′	104°00′	6	–	...	...	9–11	9.2	...	...	12–14	13.0
ROM17834	Echo L.	50°00′	106°00′	44	–	0–5	0	8–10	9.3	1.5–2.1	1.8	12–14	13.3
ROM19083	Cree L.	57°30′	107°00′	15	–	0–2	0	8–10	9.4	1.0–2.0	1.7	12–14	13.2
ROM19077	Wollaston L.	58°00′	103°30′	30	–	0–3	0	7–11	8.9	...	...	11–14	13.0
ALBERTA:													
BC57-354	Calling Lake	56°20′	113°00′	4	–	...	0	9–10	9.2	...	...	13–14	13.4
BC56-7	Cold Lake	54°30′	110°20′	4	–	...	0	9–10	9.5	...	...	12–14	13.0
NMC58-149	Ft. Chipewyan	58°40′	111°00′	22	–	0–2	0	8–10	9.2	1.2–1.6	1.4	12–15	13.3
BRITISH COLUMBIA:													
BC60-356	Ft. Nelson R.	58°40′	122°30′	1	–	...	0	...	9	...	...	...	...

Red and White Muscle of Fish in Relation to Rigor Mortis[1]

By Hans Buttkus

Fisheries Research Board of Canada
Technological Station, Vancouver 8, B.C.

ABSTRACT

The superficial red muscle of lingcod (*Ophiodon elongatus*) was shown to exhibit unique operties of post-mortem contraction and tension development. In comparison with white uscle, rigor contraction and isometric rigor tension in red muscle were about three times as eat. The rate of contraction of the red muscle was dependent on temperature and also on the ygen concentration in the surrounding atmosphere. The elastic modulus of the red muscle trout and lingcod increased with increasing post-mortem time. Following the onset of rigor ortis a gradual increase in elasticity was observed. The maximum effects of contraction, tension d elasticity coincided with the onset of rigor mortis and each could therefore be used as a easure of this phenomenon. It was concluded from these experiments that stiffening of a fish ith the onset of rigor mortis is not due to contraction or tension development of the muscles, t rather to their changing mechanical properties. A convenient measure of the changing echanical properties in the muscle was the elastic modulus.

Morphological differences between the very active, myoglobin rich, red muscle and the white uscle of lingcod were demonstrated by means of electron micrographs. The high glycogen ntent in the area of sarcoplasm of the red muscle, as indicated in electron micrographs, was nfirmed by chemical analysis. Red muscle in rested fish was shown to contain from 1 to 3 nes more glycogen than white muscle.

INTRODUCTION

HE FIRST MAJOR post-mortem changes in the appearance and structure of fish uscle become noticeable with the development of rigor mortis. The importance rigor mortis as an influence on the keeping properties of fresh fish and on the ality of frozen fish has been realized and some work on this subject has been viewed by Amlacher (1961). Generally the progress of rigor mortis has been aluated by observing the degree of post-mortem stiffness. More refined echanical devices have been developed by Messtorff (1954), and Nemitz *al.* (1960) which measured changing elastic properties of fish muscle. Noguchi d Yamamoto (1955) utilized muscle contraction, caused by perfusing water, to termine rigor. In the present work the relative contribution of red and white uscle to the physical changes taking place in a fish during rigor development re investigated. By observing the changing characteristics of contraction, nsion and elasticity of the red and white muscle, the progress of rigor could followed.

The terms rigor contraction and rigor tension in the present paper are used describe post-mortem contraction and tension development of a muscle which e not produced by electrical or other external stimuli. The duration of such

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[1] Received for publication June 26, 1962.

Fish. Res. Bd. Canada, **20**(1), 1963.
inted in Canada.

a contraction and tension development is from the time almost immediately post mortem to the onset of full rigor mortis. The modulus of elasticity is a measure of the elastic properties of the muscle. Since it is inversely related to the extension of the muscle under a certain force, the value of the modulus will be comparatively small when the muscle is still very elastic, immediately post mortem. Approaching rigor mortis, however, the muscle becomes increasingly rigid and its ability to stretch under force decreases. The modulus of elasticity of a muscle will therefore increase as it approaches rigor mortis.

METHODS AND MATERIALS

The lingcod (*Ophiodon elongatus*), 1–2.5 kg, used in the present experiments were caught at sea by trawl net and kept at the Vancouver Public Aquarium. When needed for an experiment, they were transported to this laboratory in sea water maintained at about 12°C, under constant oxygen supply and with care to prevent excitement of the fish. They were then killed by stunning.

Red muscle to be used in contraction, tension and elasticity experiments, was obtained from one side of a freshly killed fish. After removing the skin with a sharp knife, portions of 10.0 and 5.0 cm of the red muscle were marked off along the axis of the fish with wood splinters. After leaving an additional length at each end for attachment to the lever and plastic vice, the sections of red muscle were dissected quickly from the fillet. Marking of the original length of the muscle in the body of the fish was done in order to express the contraction of the muscle relative to this length. This was especially necessary in exhausted or exercised fish, where a very marked contraction takes place during and after dissection. The white muscle used in these experiments was cut from the lower portion of the epimere, where the arrangement of fibers is similar to the red muscle. For the contraction experiments with a kymograph and lever arrangement, about 1.5 cm wide and 10.0 cm long strips of red and white muscle were used. One end of the muscle was clamped into a plastic vice and suspended in a humidity chamber. A silk thread was tied to the lower end of the muscle and attached to one end of an aluminum lever. The changing length of the muscle was thus recorded with an ink pen on a kymograph drum turning at 2.2 revolutions per day. Penetration measurements were made simultaneously with a Mangold sclerometer (Mangold, 1922) on a section of white muscle only, a portion of white muscle with red muscle attached to it and a section of red muscle only.

To measure the elastic modulus and the work potential, the red muscle of trout and lingcod was cut into strips 1.0 cm wide and 5.0 cm long. They were loaded within their elastic limit and unloaded every 15 minutes for 15 seconds as described for mammalian muscle by Bate-Smith and Bendall (1948, 1949) and Marsh (1954).

Tension development in red and white muscle during isometric rigor contraction was followed with an experimental arrangement as shown in Fig. 1A and 1B. A strip of muscle, 5.0 cm long, dissected from a freshly killed fish was suspended between the plastic vice and the lever. At the opposite arm of the lever was fastened a strong silk thread, leading to the plate shaft of the Mechano-

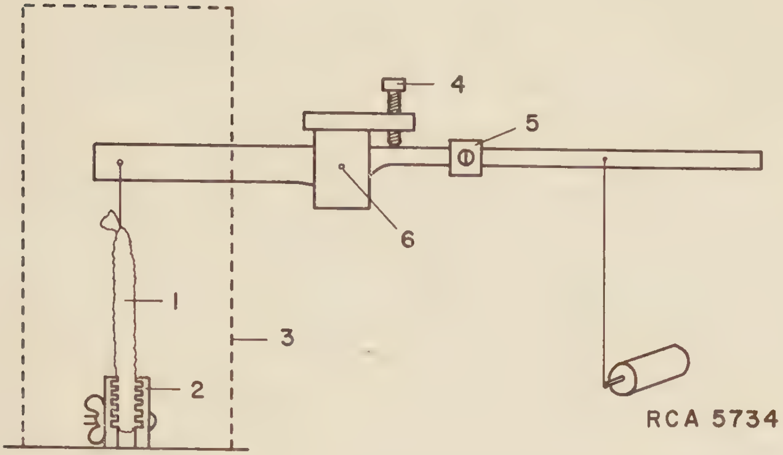

FIG. 1A. Apparatus for measurement of tension development in red and white muscle during isometric rigor contraction. (1, muscle; 2, plastic vice; 3, humidity chamber; 4, stop screw; 5, rider weight; 6, fulcrum.)

lectronic Transducer RCA 5734 (Donaldson, 1958). The weight of the attached uscle was balanced with a rider weight. After the muscle had been suspended the apparatus, the lever action was arrested by a stop (see Fig. 1A) so that o tension was transferred to the plate shaft of the transducer tube. At this etting, the electronic circuit (Fig. 1B) was balanced. The galvanometer was hen disconnected from the circuit by means of a throw switch and the stop crew withdrawn so that the tension in the muscle could be freely transferred via he lever to the input transducer. The potential drop across resistor (R_v), aused by the imbalance of the bridge circuit, could then be measured with a otential recorder. The instrument was zeroed before every tension measure-ent. At the beginning and the end of an experiment it was calibrated against eights from 1.0 to 15.0 g.

During all the contraction, tension and elasticity experiments, the excised uscle strips were kept in a humidity chamber. The remaining portion of the sh, from which only one side of the lateral muscle had been dissected, was rapped in polyethylene and held as a control at the same ambient temperature t which the experiments were conducted. Comparisons between the amount f contraction, the elastic modulus or the tension development in the excised uscle and the stiffness of the remaining fish could be carried out in this manner.

Humidity chambers were adapted for the different lever devices. They were uilt from Plexiglas and partially lined with Whatman No. 17 filter paper. he filter paper was kept saturated with water during the experiments. Connec-ons into these chambers were provided so that water saturated oxygen or itrogen could be introduced during some experiments. For certain experiments, onducted at an ambient temperature of 0°C, a heating coil was inserted into e humidity chamber. In this way the temperature of the excised muscle could e adjusted to the temperature of the slowly cooling fish.

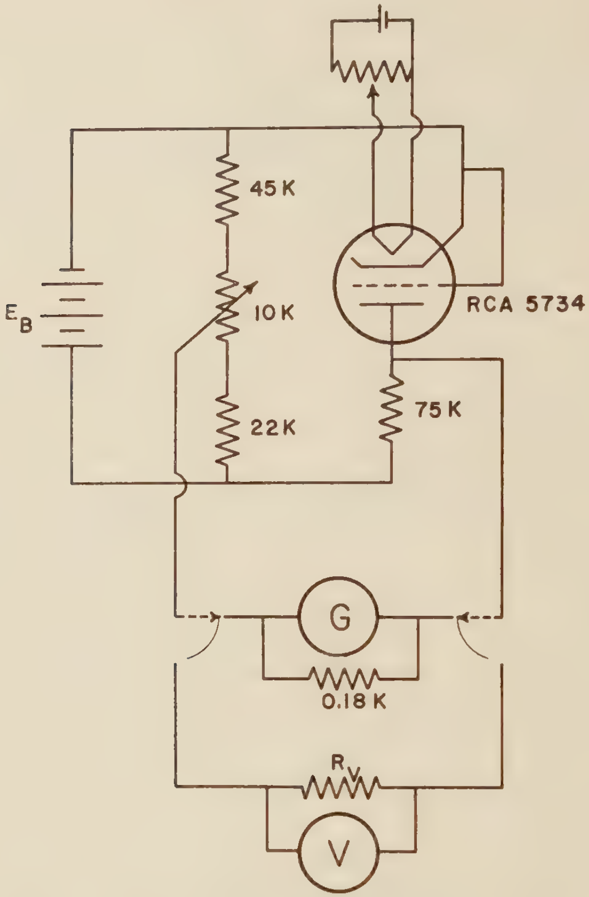

Fig. 1B. Circuit diagram; the Mechano-Electronic Transducer RCA 5734 was connected in a Wheatstone type bridge circuit operated at $E_B = 200$ volts obtained from a Heathkit Regulated Power Supply, Model P.S.4. The filament current was supplied by a 6-volt storage battery. R_v was either 470 or 1100 Ohms, depending on the force applied to the plate shaft.

Glycogen analyses were carried out on rested, feeding fish. They were killed by stunning and the red and white muscles were immediately dissected at 0°C. Portions of 1.0 g were weighed into cold centrifuge tubes. After adding 7.0 ml 30% KOH per 1.0 g of red muscle and 3.0 ml 30% KOH per 1.0 g of white muscle the tubes were immersed for about 20 min in a boiling water bath. Glycogen was precipitated with 1.2 volumes of ethanol. The precipitate was washed once with ethanol and the glycogen was determined by the methods of Montgomery (1957) and Carroll *et al.* (1956).

Fillets to be used in thaw rigor experiments were obtained from freshly killed fish which had been treated in much the same way as described above. The

ets were stored immediately in plastic bags at –30°C. After a few days of
rage they were cut into blocks about 4 cm² top area. The red muscle on the
face of the fillets was cut off some blocks and left in position on others.

RESULTS AND DISCUSSION

GOR CONTRACTION

It was found during cold storage studies of fish fillets that the contraction
ed muscle during thaw rigor is more pronounced than that of the white muscle.
en pieces of frozen fillets from which the red muscle had been cut off were
wed at room temperature, the total contraction in length amounted to 13%.
rose to as much as 33% on pieces of fillets which contained white and red
scle. Such a large decrease in length, on a section of white and red muscle,
ulted, however, at the same time in an increase of height so that the actual
ume shrinkage remained comparatively small. The large alteration of
ension which such a muscle block underwent during thaw rigor resulted in an
reased exudation of drip. The drip from white muscle only amounted to
% ±1.0, whereas that from pieces where white and red muscle had not been
arated amounted to 10.5% ±1.4.

It seemed therefore interesting to determine the contraction characteristics of
and white muscle in the course of normal rigor development, i.e. post-mortem
ditions leading to rigor at room temperature.

The contraction studies of red and white muscle with a kymograph and lever
angement showed that the red muscle contracted 52% of its original length
en going into rigor at 20°C, white muscle only 15% (Fig. 2). As can be seen
m the graph, after the point of maximum contraction has been reached, a small
definite extension of the red as well as white muscle proceeded with time.
nerally, a definite decrease of rigor tension (softening) in the control fish was
iceable after about 24 hours. Following the initial point of maximum rigor,
nall decrease in the elastic modulus of the red fish muscle was also noted with
experimental arrangement described by Bate-Smith and Bendall (1948).
is fact may account for the slight but definite resolution of rigor mortis in fish.
ef muscle, on the other hand, when held after the development of rigor at 7°C
7 days in nitrogen showed no increase in extensibility (Marsh, 1954).

Of particular interest during these studies was the question whether the
ximum contraction of an isolated muscle would coincide with the beginning
naximum rigor hardness of the fish from which the muscle had been excised.
vas found that the point of maximum contraction of the red muscle, as measur-
with a lever and kymograph arrangement, often preceded the beginning of
rigor in the control fish, sometimes by as much as 1 to 1½ hours. The larger
control fish, the larger was the observed time difference. Since the rate as
l as the intensity of contraction and tension development was shown to be
ongly temperature-dependent (compare Fig. 2 curve A and those of Fig. 3),
effect was ascribed to the difference in temperature between the isolated
scle strip and the control fish. Although both were kept at the same ambient
perature, the comparatively small muscle strip would soon reach the tem-
ature of its surroundings while it took the larger fish very much longer to

come to temperature equilibrium. When the rate of temperature rise in the dissected muscle was adjusted to that of the control fish, maximum contraction or tension development did coincide with the onset of maximum rigor stiffness in the control fish.

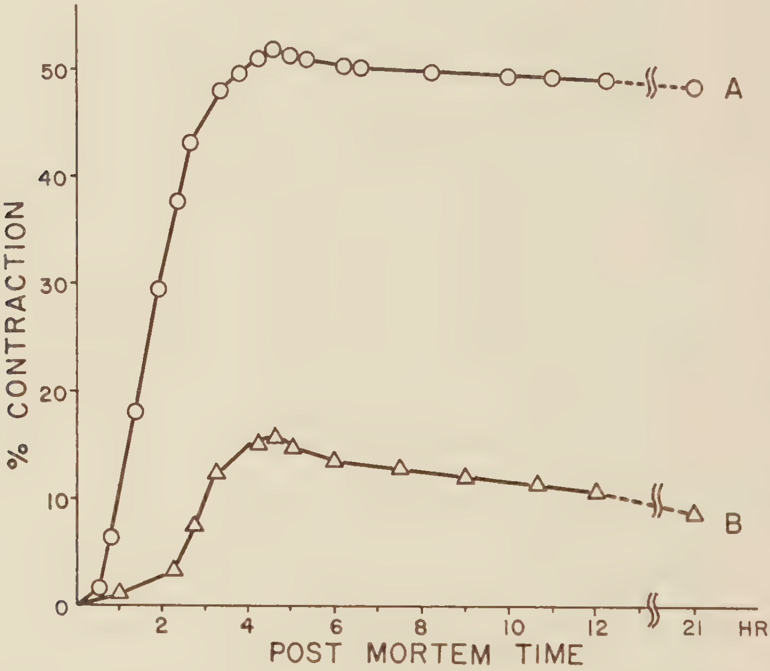

FIG. 2. Rigor contraction of excised red (O–O) and white (△–△) muscle of lingcod at 20°C.

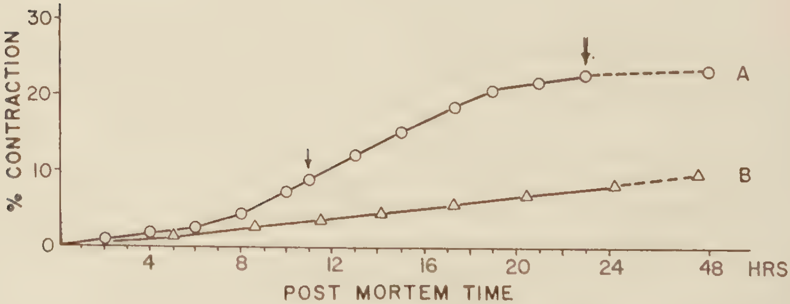

FIG. 3. Rate of rigor contraction of the superficial red muscle of lingcod at an ambient temperature of 0°C. Curve A represents the contraction of excised red muscle in air. The temperature of the excised muscle was adjusted to the temperature 1.0 cm below the skin of the cooling fish. It dropped from 12.6° to 2.6°C in 11 hours. Curve B: the red muscle was cooled to 0°C immediately after dissection. (↓ first signs of stiffening are detectable in the control fish; ⇓ full rigor is established, the whole fish is quite rigid).

The rate of contraction of the red muscle could further be influenced by rounding the excised muscle with an O_2 or a 95% N_2 + 5% CO_2 atmosphere ig. 4). From the origin to point (A), two strips of muscle, obtained from the ne fish, were contracting in air at an equal rate. Thereafter a flow of water-urated oxygen was introduced into one humidity chamber and a mixture of rogen and carbon dioxide into the other. The rate of contraction of the muscle the oxygen atmosphere decreased to about half that of the muscle contracting der anaerobic condition. The limiting factor of this phenomenon is probably diffusion of oxygen into the muscle. After the oxygen flow was turned off (B), contraction of the muscle accelerated again. These experimental facts m to indicate that rigor contraction is promoted by a lack of oxygen required

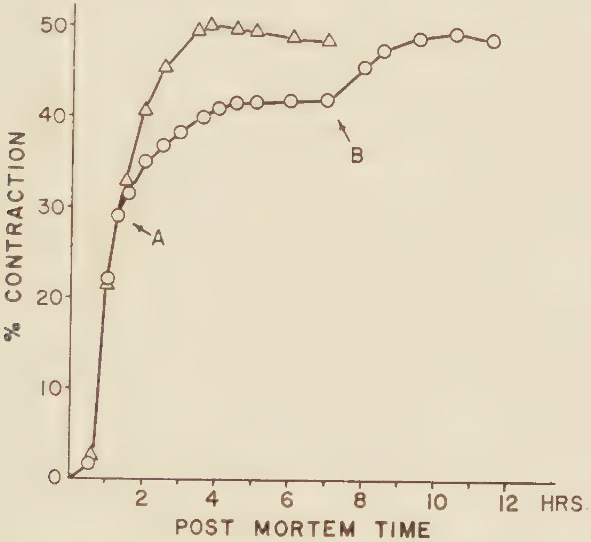

FIG. 4. Rate of rigor contraction at 20°C as affected by the atmosphere surrounding the muscle. The rate of contraction of one piece of red muscle was measured in an O_2 atmosphere (O–O) while the other was suspended in 95% N_2 and 5% CO_2 (△–△). (A): Gas flow of (N_2 + CO_2) or O_2 is introduced into the respective humidity chamber. (B): Flow of O_2 into the humidity chamber is turned off.

certain reactions in the cell, or by products of anaerobic metabolism. Forty- years ago Fletcher and Hopkins (1917) showed that no lactic acid was formed muscle kept under oxygen and that the stiffening of early rigor mortis dis- eared in an oxygen atmosphere. Today, the first fact is easily explained as eased metabolism of carbohydrate by the Embden-Meyerhof pathway. e oxygen functions to a large extent as hydrogen acceptor in the last stage iological hydrogen transfer systems, a lack of oxygen would lead to an ac- ulation of reduced metabolic intermediates and a decreasing resynthesis of adenosine triphosphate (ATP) would also be imminent. However, a direct connection between known biochemical processes and rigor mortis is still lacking.

Post-mortem tension development during isometric rigor contraction was shown to be more pronounced in red than in white muscle (Fig. 5). The intensity of the maximum effect varied with different fish, presumably in different nutritional conditions. In four samples of red muscle the maximum rigor tension ranged from 14.3 to 19.1 g wt./2.3 g of muscle, and in white muscle it ranged between 4.2 to 6.0 g wt./2.3 g of muscle. Tension development decreased with decreasing temperature. At 7°C the maximum rigor tension in red muscle decreased to 3.9 g wt./2.3 g of muscle and coincided with the onset of full rigor in the control fish, 22 hours post mortem. It is interesting to note that tension development, especially in red muscle, did not proceed as smoothly as contraction but fluctuated considerably while approaching maximum rigor. It appeared as if the muscle was cycling between periods of exhaustion and recovery. Four hours post mortem, after the peak of rigor tension had been reached, the muscle seemed to go into a state of pronounced exhaustion, and tension decreased very rapidly to a minimum. The following recovery and exhaustion periods gradually decreased in tension and were found after 24 hours post mortem in the region of 1.0 g wt. of tension.

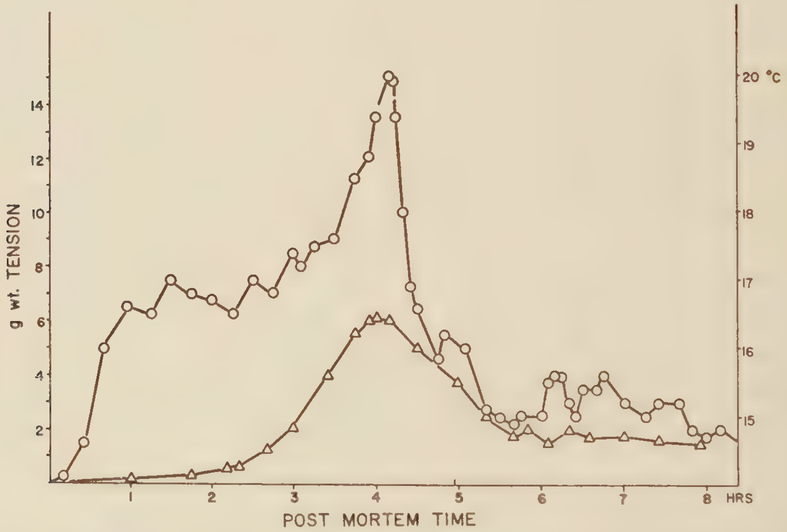

FIG. 5. Tension development during isometric rigor contraction in 2.3 g of white (△–△) and 2.3 g of red (O–O) muscle of lingcod at 20°C.

The changes in tension could only partly be related to the presently accepted biochemical knowledge on post-mortem changes in muscle (Szent-Györgyi, 1945; Bate-Smith and Bendall, 1948, 1956). In pre-rigor muscle ATP, the most immediate known source of contraction energy, is at first maintained, then slowly creases until it drops to a very low value at full rigor. Presumably, following e rigor peak (Fig. 5), no further sources of energy-rich phosphate were available d the forces which the muscle was able to exert decreased to a minimum until e ATP resynthesized was sufficient for another but comparatively small increase d so on. However, why the muscle exerts its maximum tension just before ing into rigor, when the ATP concentration is reaching a low, limiting value, nnot be explained at the present time. It may be an indication that rigor ntraction and tension are not equivalent with contraction and tension develop-ent under optimum physiological conditions. Post-mortem contraction of uscle can also be brought about by contact with acids (lactic acid amongst hers; Fletcher and Hopkins, 1917), addition of monoiodoacetate, or by prolonged imulation with caffeine or chloroform-vapour, etc. (Szent-Györgyi, 1945).

ODULUS OF ELASTICITY

Bate-Smith and Bendall (1948) and Marsh (1954) have described and used method to follow the changing elastic modulus in mammalian muscle with creasing post-mortem time. Since the short fibers of white fish muscle were t considered suitable for such measurements, comparative studies on this basis ve never been carried out on fish. Red muscle fibers, however, are arranged ore uniformly in one direction. This made it possible to compare the elastic odulus and work potential of the red muscle of fish to mammals. Measure-ents were carried out immediately post mortem, through the development of gor mortis and its resolution. At 6.52% initial extension of the red muscle of 250-g trout (*Salmo gairdnerii*), the elastic modulus was found to be 980–1020 cm² (0.98 × 10^6 dynes/cm²) and increased in rigor to 6000 g/cm² (5.9 × 10^6 nes/cm²). With the onset of rigor, the modulus of elasticity increases. For bbit muscle (psoas) it rises from 500 to about 10,000 (Bate-Smith and Bendall, 49); for beef (*Longissimus dorsi*) from 1110 ±270 to 34900 ±1770 (Marsh, 54), for chicken (*Pectoralis major*) from 1000 to 9000 at 14°C or 2000 to 8000 cm² at 43°C (de Fremery and Pool, 1960). The work potential of the red teral muscle from the same trout was found to be 2.3 g cm/g at 20°; that of bbit is reported to be less than 1.0 and of beef 3.6 g cm/g at 17°C.

Measurements of the elastic modulus on the red muscle of trout agree well th physical data obtained from whole trout by Nemitz *et al.*, 1960. They termined the ratio of the torsion moduli G_z at time z to G_o immediately post ortem, by measuring the angle of torsion ψ_z at time z and ψ_o immediately post ortem, since

$$\frac{G_z}{G_o} = \frac{\psi_o}{\psi_z} = S.$$

cording to the equation $E = G2(1 + \mu)$, the modulus of elasticity E is directly oportional to the torsion modulus G. If, therefore, the difference between the isson ratio μ, for muscle immediately post mortem and during rigor mortis, is ly small the above relation can be extended to

$$\frac{E_z}{E_o} \eqsim \frac{G_z}{G_o} = \frac{\psi_o}{\psi_z} = S.$$

Actual measurements of the Poisson ratio yielded values such as $\mu = 0.29$ immediately post mortem and $\mu = 0.18$ during rigor mortis. The ratio of the elastic moduli

$$\frac{E_z}{E_o} = 6$$

as measured during our experiments ($E_z = 6000$ g/cm^2 during the height of rigor mortis and $E_o = 1000$ g/cm^2 immediately post mortem), falls well within the range of Nemitz and Partmann's S values for trout (*Salmo irideus* Gibb) which vary between 4.7 and 7.5.

THAW RIGOR

Thaw rigor contraction of red muscle (Fig. 6) is much greater at room temperature than that at 3°C. Defrosting and rigor contraction at the lower temperature were complete after five hours. During this time the muscle had contracted 12%. Even after raising the temperature to 20°C, as indicated by

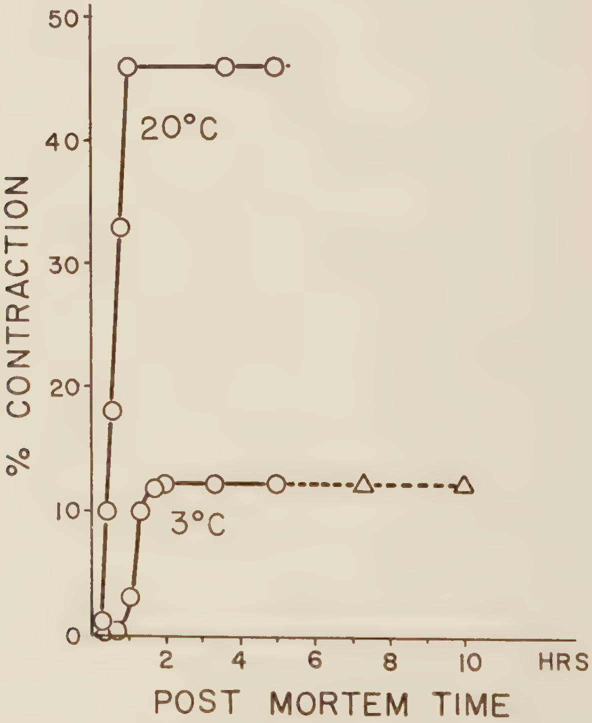

FIG. 6. Rate of contraction of red muscle during thaw rigor. Red muscle of lingcod was dissected, wrapped in aluminum foil and immediately frozen at –30°C. Two days later, it was suspended in a humidity chamber and defrosted at 20 and 3°C. No further contraction took place in the defrosted muscle after it was removed from 3 to 20°C (– – – △).

dotted line, no further contraction took place. Marsh (1958) on studying thaw or in lamb found that pre-rigor muscle frozen at −70°C and stored at −3.5°C four days did not shorten or release drip when thawed at 16°C. He concluded it during such a procedure the temperature is sufficiently high to allow the emical changes to proceed, yet enough ice remains to maintain shape and idity.

Penetration measurements with a Mangold sclerometer showed that during or mortis at 20°C, the superficial red muscle of lingcod attains a hardness nost as great as that of rabbit muscle. The increase of hardness in the white iscle was, however, very much less.

NERAL DISCUSSION

The comparative role of contraction, tension and elasticity in post-mortem iscle to the development of rigor mortis in fish remains unexplained. All ree are obviously closely related to rigor mortis, since their maximum effects ncided with the development of maximum stiffness in the control fish. However, which of these effects is involved in producing stiffness cannot be stated th certainty. Tension development can be eliminated as a factor, since it creases immediately following the onset of rigor while the control fish remains ff for hours after this point. Bate-Smith and Bendall (1956) in their studies rabbit muscle, state that while considerable shortening sometimes occurs ring the rapid phase of rigor, this shortening is not a necessary concomitant of ffening and rarely occurs under the normal conditions of rigor at room temrature (10–25°C). For red muscle of lingcod and trout, however, post-mortem ntraction at 20°C is a consistent phenomenon. The rate of contraction can en provide information as to the condition of the fish before death. Thus, if a h is exhausted before killing, the muscle seems to become "activated" and ntracts at a higher rate, with consequent more rapid development of maximum ntraction and rigor than in a rested fish. If the temperature dependence of ntraction is considered, however, it cannot be accepted as the cause of stiffen-, because when the amount of contraction in the red muscle is reduced to less an half (Fig. 3 curve A), the stiffness of the control fish is not reduced by one lf. In fact, the stiffness attained in rigor at an ambient temperature of 0°C, almost as great as that at 20°C.

Although contraction and tension do not produce stiffening, they do proceed rallel to the development of rigor mortis. At the height of contraction and nsion development, i.e. the onset of full rigor mortis, significant changes take ice in the mechanical properties of the muscle. Such changes must originate the molecular level of the structural units of the muscle and have been explained the formation of the actomyosin complex (Szent-Györgyi, 1945), or by the sociation of contractile filaments by weak cross linkages (Bate-Smith, 1948). ie increasing elastic modulus, measured during the development of rigor mortis, then probably a measure of the changing structural properties of the proteins the fish muscle.

The unusual properties of contraction and tension development shown by the myoglobin rich red muscle suggest that it is a very active tissue which might exhibit major biochemical differences from white muscle. In this laboratory, Bilinski (1962) found that oxidation of some fatty acids takes place at a very much higher rate in red than in white muscle. The ATP content of red muscle was found to be lower than that of white muscle (Saito *et al.*, 1959). He also found that inosinic acid is decomposed more rapidly in red muscle, leading to an increase in inosine, and eventually hypoxanthine and ribose. The lipid content of red muscle of cod was found to be 2% as compared to 0.7% in adjacent white meat (Fraser *et al.*, 1961). In mackerel, herring and halibut, the total lipid content of such muscle was reported to be as high as 27 to 29% (Braekkan, 1959). In his work on the B-vitamin content of red muscle he suggested that this muscle acts as a supplementary liver rather than as a contractile organ. Braekkan felt that muscle with such high fat content is scarcely suited for strenuous and continued activities. However, the unusual contractile properties of the superficial red muscle of lingcod and trout as found in the present work do not seem to warrant its exclusion from the muscular tissue responsible for locomotion. The location of the main portion of the red muscle along the lateral line, its penetration to the spinal cord, as well as its aligned direction from head to tail, would seem to indicate that it is an active component of a fish's muscular equipment which is designed for rapid acceleration.

ELECTRON MICROSCOPY

Small strips of the superficial red muscle and dorsal white muscle of lingcod (*Ophiodon elongatus*) were excised immediately after the fish was killed. The small sections of muscle were fixed in a 1% solution of osmium tetroxide adjusted to pH 7.4 with veronal-acetate buffer. After 2½ hours of fixation, small pieces were cut from the blackened layers of the muscle. These pieces of tissue were dehydrated in a series of increasing concentrations of ethyl alcohol and embedded in epon according to the procedure of Luft (1961). Sections were cut with a diamond knife on a Servall microtome. Those displaying yellow interference colors were selected for examination, floated on collodion-coated copper grids and stained with lead hydroxide (Watson, 1958). The sections were stained in a nitrogen atmosphere by floating the grids face down for 10 minutes on the surface of the lead hydroxide solution. They were washed in decarbonated, distilled water and dried on blotting paper. Electron micrographs were made with a Siemens instrument.

Electron micrographs of the red muscle of lingcod (Plate 1) show the characteristic arrangement of myofibrils. The difference in the fine structure of this muscle, as compared to white muscle (Plate 2) and skeletal muscle from rabbits (Huxley, 1960), lies in the region which is normally described as the A-band. The H-zone, present in all types of relaxed skeletal muscle of vertebrates and invertebrates, is very indistinct or not visible in these electron micrographs of the red muscle of lingcod. The fine structure of the white muscle of lingcod shows essentially all the characteristic features of skeletal muscle of rabbit.

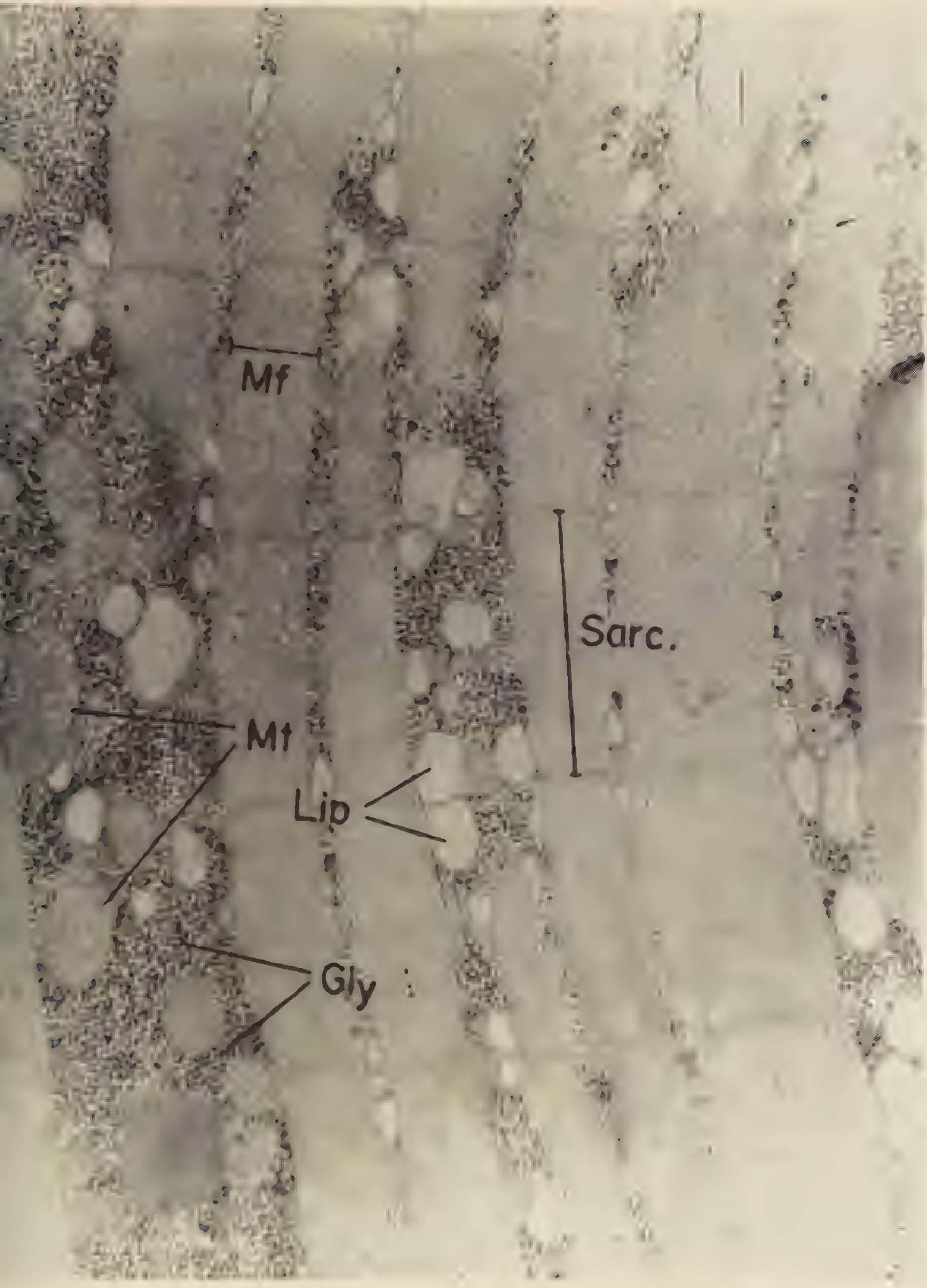

PLATE 1

Superficial red muscle of lingcod 12100 diameters.

Abbreviations.—Gly, Glycogen granules; Mt, Mitochondria; Mf, Myofibril; Lip, Negative ages of fat droplets dissolved during preparation of specimen; Sarc, Sarcomere, segment of ofibril between two Z-lines.

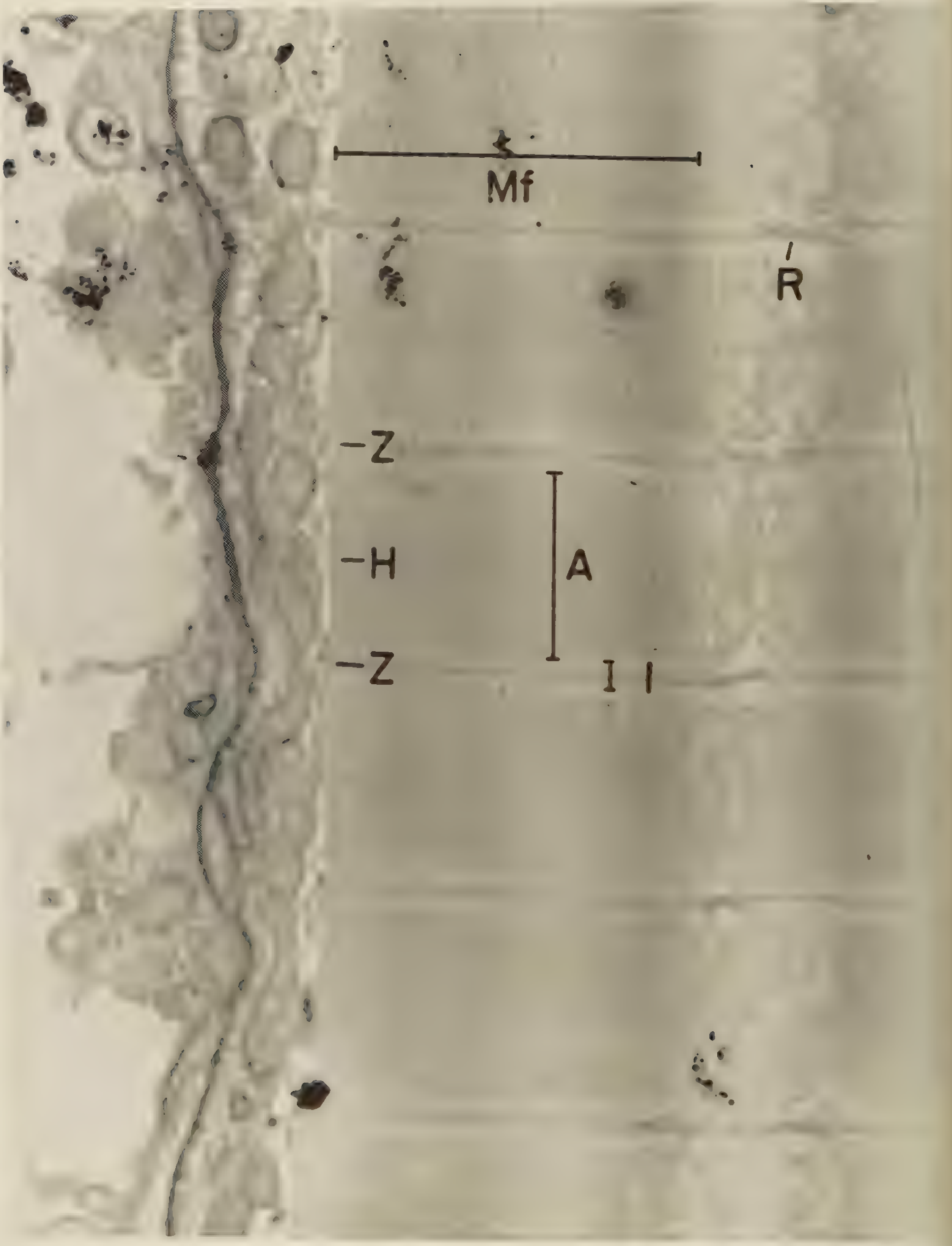

PLATE 2

White dorsal muscle of lingcod 12100 diameters.

Abbreviations.—A, A-band; I, I-band; H, H-zone; Z, Z-line; R, attachment of reticulum to Z-line; Mf, Myofibril.

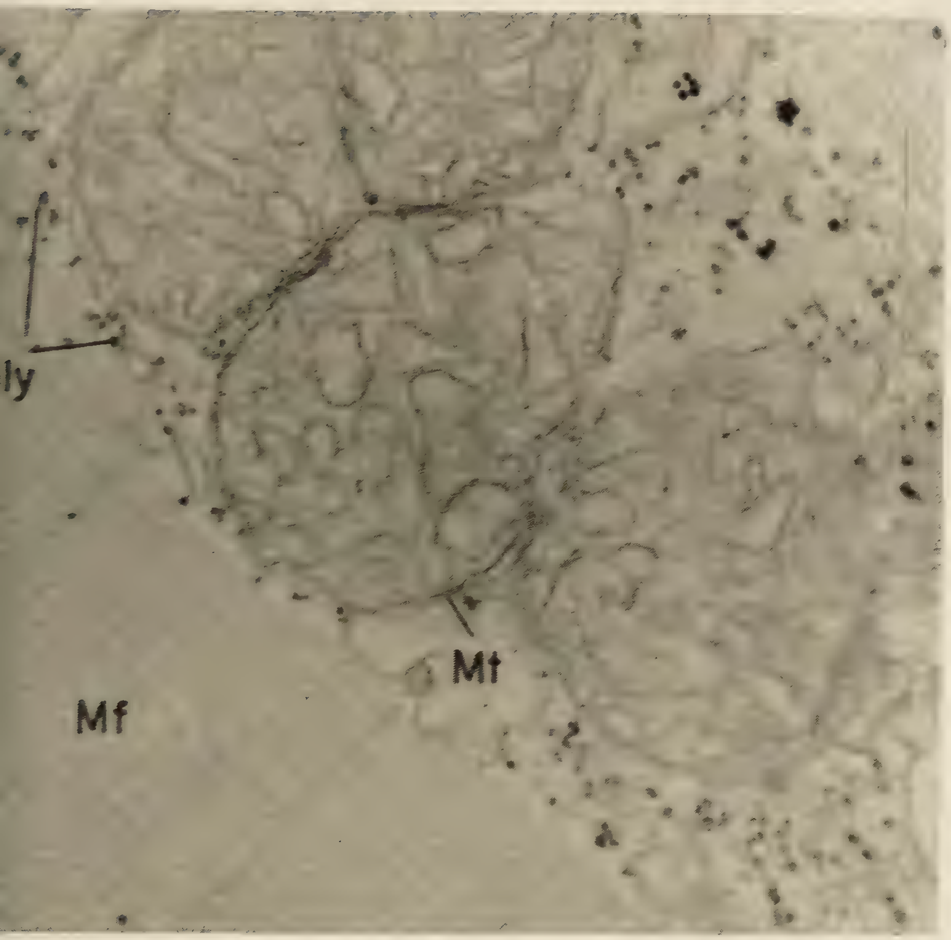

PLATE I

White dorsal muscle of lingcod, 37200 diameters.

Abbreviations: Gly, glycogen; Mt, mitochondria; Mf, Myofibril

he proportions of the bands are, however, different. The I-band, in the white uscle of lingcod, is very much shorter while the A-band is proportionately onger, taking up 85% of the sarcomere length. The mitochondria in the two ifferent muscles show also a different structure. Those in the red muscle seem o be of the characteristic cristae type found in mammals. The mitochondria n the white muscle (Plate 3) seem to possess a more tubular structure.

Treatment of tissue sections with lead hydroxide increases the electron ensity of the glycogen granules. Studies on the morphological identification f thus stained glycogen have been conducted by Revel *et al.* (1960). The arcoplasmic area of the red muscle of lingcod (Plate 1) can be seen to contain very much higher density of glycogen than that of white muscle (Plates 2 and). To confirm this observation by chemical analysis, red and white muscles of ested, feeding fish were assayed for their glycogen content. This was found to ary in white muscle from 0.35 to 0.51% and in red muscle from 0.55 to 0.98%. owever, the pH at the height of rigor mortis was not observed below 6.5 in the ed muscle.

ACKNOWLEDGMENTS

I wish to thank Dr H. L. A. Tarr for his interest and encouragement, and or his help and suggestions in preparing the manuscript.

Special thanks are extended to Dr W. H. Chase, University of British olumbia, Faculty of Medicine, Department of Pathology, for his advice, nstructions and help in obtaining the electron micrographs.

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Estimation of Catchabilities and Population Sizes of Lobsters[1]

BY J. E. PALOHEIMO

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

Techniques of estimating population size, level of fishing, and the degree of dependence of shing success on environmental factors are examined on the basis of tagging, catch and effort ata. A new method is developed to estimate population size from catch, effort, and temperature ata when the catchability varies with temperature.

The methods of estimation discussed are applied to data collected from a number of lobster sheries on Canada's Atlantic coast. Analysis confirms a relationship between the catchability lobsters and bottom temperature. Differences in this relationship are found between areas nd between tagged and untagged lobsters within areas. It is suggested that these differences e attributable to the differences in densities as well as to aggregations of lobsters and fishing. he effect of these aggregations on population size estimates is considered.

Calculated average catchabilities at comparable temperatures are different for different eas. These differences are correlated with the numbers of trap hauls per day per square miles shed. It is suggested that the differences in the catchabilities might be due to interactions etween units of gear not predicted by the customary relationship between catch and effort.

INTRODUCTION

OPULATION SIZE, levels of fishing, and dependence of fishing success on environental factors such as temperature are important basic parameters in the study f natural fish populations. In this paper we describe two distinctly different ypes of techniques for determining them, and study their application to commerally fished lobster populations on Canada's Atlantic coast. In the first place, e have derived formulae which permit the use of tagging and catch data to rrive at estimates of population sizes, catchabilities and levels of fishing. Relavely simple formulae are proposed because statistically elaborate models are ore sensitive to deviations from the basic assumptions. Estimates obtained by e use of tagging and catch data may also be obtained from catch, effort, and mperature data. A new method of estimating these parameters from the latter ype of data is developed. In effect it is a modification of the catch-per-effort ethod developed by Leslie and Davis (1939) and DeLury (1947, 1951) llowing the catchability to vary with temperature.

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[1] Received for publication July 23, 1962.

FISH. RES. BD. CANADA, 20(1), 1963.
rinted in Canada.

In using these methods one must first attempt to study their applicability to data. In fact, analysis of the lobster data reveals apparent differences in the rate of capture between tagged and untagged lobsters in most of our study areas. Evidence available from these data and outside information on lobster populations (D. G. Wilder, 1947, 1953, 1954, and personal communication) suggest that these differences are related to clustered distributions and to the slow rate of mixing of tagged and untagged lobsters rather than to the physical effect of tagging operations on lobsters. These differences have an effect of biasing tagging-recapture estimates of population size. Moreover, the postulated non-uniform distribution pattern of lobsters also leads to bias in estimates of population size based on catch, effort, and temperature data.

In general the bias works in the opposite direction for the two different methods. In areas where the rate of capturing tagged and untagged lobsters is not markedly different, the two methods should give reasonably similar estimates. This was verified by the calculations for one of the study areas where the above conditions were met.

Description of the Fishery

Lobster fishing in Canada is regulated in a number of ways. The whole Atlantic coast is divided into lobster districts. In each district lobster fishing is allowed only during a restricted season, although the seasons in different districts are staggered to ensure some landings at all times during the year. The sizes of lobsters that fishermen are allowed to land are regulated by a minimum legal-size limit. This limit varies from area to area.

The fishery is primarily an inshore fishery, extending usually no more than 2 to 6 miles from the coastline. The boats used are open, motor powered, and mostly less than 45 feet in length. Wooden lobster traps are used almost exclusively as fishing gear. They are half-cylinder shaped with netting at both ends, so arranged to facilitate entry of lobsters into the trap but to impede exit.

To provide information on the fishery, the Fisheries Research Board of Canada has been collecting data under the direction of Dr D. G. Wilder in a number of commercially important lobster areas. These areas characteristically contain one fishing port or a wharf where most of the lobster boats are docked and where most of the lobsters are landed. The area where boats from this central port concentrate their fishing is then mapped out and designated as a study area. In some instances, more than one port has been included in the study area in which case all ports are covered in the sampling. Since lobsters are relatively non-migratory (Wilder and Murray, 1956, 1958), we have considered the population in each study area as an isolated unit.

The five major areas studied by the Biological Station, St. Andrews, N.B., and analysed here are Miminegash and Tignish, Prince Edward Island, and Fourchu, Gabarus, and Port Maitland, Nova Scotia. Areas are named by the main port. The areas are described in Table I. For more detailed descriptions, the reader may consult publications by Wilder. Earlier studies in these areas include those by Smith (1944) and by Templeman (1935, 1936).

TABLE I. Characteristics of lobster study ports.

	Tignish, P.E.I.	Miminegash, P.E.I.	Gabarus, N.S.	Fourchu, N.S.	Port Maitland, N.S.
Location:	North side, P.E.I.	Northumberland Strait.	East coast Cape Breton.	East coast Cape Breton.	Southwest tip Nova Scotia.
Type of bottom:	Broken bottom. Mainly sandstone rocks.	Broken bottom. Mainly sandstone rocks.	Very uneven. Granitic rocks and metamorphosed sediments. Many shoals and islands.	Uneven. Granitic rocks and metamorphosed sediments.	Uneven rocky bottom of quartzite and slate.
Offshore fishing limit (miles):	3–6	3	2	1–4	7½
Area in square nautical miles:	55	25.6	21.4	20.8	32.5
Depth of water (fathoms):	2–12	1–12	4–16	4–18	4–30
Seasons:	May 1–June 30	Aug. 10–Oct. 5	May 16–July 15	To and incl. 1946, and 1953 onwards, May 16–July 15 (1947–52, May 20–July 15)	Dec. 1–May 31
Median carapace length (inches):	2.91	3.16	3.38	3.50	4.59
Size limit in force in 1958 (carapace length):	2.50	2.50	2.75	3.19	3.19
Kind of boats:	25′ to 42′ motor boats.	25′ to 38′ motor boats.	Half of the fleet were dories and half 25′ to 30′ motor boats.	2 or 3 dories and 25′ to 45′ motor boats.	30′ to 40′ motor boats.
No. of boats:	71–120	29–59	48–71	13–36	25–44
Kind of traps:	2½ ft to 3 ft. 2 side heads. Set on trawl.	3 ft. 2 side heads. Set on trawl.	3 ft. 2 side heads. Fished singly in strings.	3 ft. 2 side heads. Fished singly in strings.	4 ft. 3 fishing heads. Fished singly in strings.

Data and Notations

The data collected in these study areas include the following statistics:

1. Daily catches (lb) per boat by market categories. In one area (Fourchu) catch statistics are available only by 2-week periods.
2. Numbers of trap hauls per boat for selected groups of boats.
3. Samples of sizes of lobsters caught and of those landed, including average weights by market categories.
4. Daily records of numbers of lobsters tagged and recaptured, and length measurements of all tagged and recaptured lobsters. In all areas studied, about 1000 legal-sized lobsters have been tagged and released uniformly over the study area either from a week to 4 weeks before the lobster season or at the latest during the first or second week of the season. The recaptures were usually reported by fishermen at the time the catch was landed. All the lobsters for tagging were obtained by the regular method of fishing from the same general grounds to which they were returned. For a description of type of tag see Wilder (1947).
5. Water (bottom) temperatures. Usually one observation per week at one or two (fixed) depths.

For the analysis, these data are grouped by one- (Tignish, Miminegash, Gabarus) or two- (Fourchu, Port Maitland) week periods. For each period the following statistics are calculated:

k number of periods in a season

C_t total number of legal-size lobsters landed during the t^{th} period, $t = 1, \ldots, k$

K_t total accumulated number of legal-size lobsters landed from the beginning of the season up to the beginning of the t^{th} period

f_t total estimated number of trap hauls made in the area during the t^{th} period

$(C/f)_t = C_t/f_t$, catch in numbers of legal-size lobsters per trap haul during the t^{th} period

c°_{t} average (bottom) water temperature during the t^{th} period, usually the average of the weekly temperature observations made at two different depths.

McLeese and Wilder (1958) have experimentally determined walking rates of lobsters at different temperatures. In their experiment the lobsters were tested at the temperatures to which they were acclimated as well as at temperatures departing from the acclimation temperature. In nature, lobsters are subject to variable temperatures and their acclimation temperatures or walking rates are not known. However, Dr McLeese has considered the thermal history of lobsters in each season as shown by our temperature records and, on the basis of knowledge of the rate of acclimation of lobsters, has estimated acclimation temperatures for each period. He has then compared these acclimation temperatures with the ambient temperatures to arrive at the walking rates of lobsters (McLeese, unpublished manuscript; McLeese, 1956). The walking rate is termed here the index of activity, a_t.

$_t$ index of activity

In addition to the above, the following symbols are used:

N_t population size of the legal-size lobsters at the start of the t^{th} period

q, q', c_0, a_0 constants

X_t estimated number of tagged lobsters in the water at the start of the t^{th} period

x_t number of tagged lobsters recaptured during the t^{th} period.

The data used in this report are tabulated in Tables II, III, and IV for those ars for which good temperature records are available. In a few cases the data ve been disregarded because something had obviously gone wrong with the gging. Thus in 1957, some of the tagged lobsters at Tignish were accidentally posed to fresh water before releasing which apparently accounts for the rather w returns (fresh water is lethal for lobsters (McLeese, 1956)). Table II gives e (estimated) total numbers of legal-size lobsters landed and the (estimated) al number of trap hauls in the study areas. Table III summarizes taggings d recaptures and Table IV gives the average bottom temperatures and the rresponding indices of activity.

METHODOLOGY

pulation Size Estimates from Marking-Recapture Data

Statistically refined methods of estimating the size of animal populations the marking-recapture method abound in the literature. These methods ually assume that the random variables, such as the numbers of tag returns the ratio of tagged individuals to the total number sampled, follow a given stribution, usually Poisson, binomial or hypergeometric. Such assumptions rmit a maximum likelihood estimate of the population size which is a best imate in the statistical sense provided, of course, that the assumptions implicit the model are satisfied.

Another approach used in the literature is to estimate population size and her related population parameters on the basis of regression or least squares ocedures (DeLury, 1951, 1958). Such an approach is perhaps more often propriate in that the estimates are not nearly as dependent on the realization particular assumptions such as that the tag returns follow a binomial or oisson distribution. Indeed we have here adopted the view that the more mplicated the model, the more sensitive the estimates are to deviations from sumptions (DeLury, 1958), hence the preference for least squares methods. ast squares estimates also permit more reliable measures of the accuracy of the sults since variability is estimated from the data rather than from the model.

The population size estimates have not been based on all tag returns, but ly on the returns after the tags had been in the water for about 2 weeks. This as done to allow the tagged and released lobsters to mix with the resident pulation.

TABLE II. Estimated total number of legal-size lobsters landed and estimated total number of trap hauls.

Year	Period	No. landed '00	No. of trap hauls	Year	Period	No. landed '00	No. of trap hauls
Fourchu				*Fourchu*			
1953	I	27	12,890	1954	I	90	14,965
	II	255	21,129		II	256	20,799
	III	192	16,890		III	296	15,628
	IV	247	18,769		IV	203	14,728
Fourchu				*Fourchu*			
1956	I	290	36,984	1957	I	163	28,282
	II	426	38,729		II	353	48,829
	III	426	38,135		III	518	47,515
	IV	252	28,979		IV	172	18,126
Fourchu				*Fourchu*			
1958	I	394	38,612	1959	I	446	48,471
	II	321	36,690		II	449	46,136
	III	318	33,132		III	136	23,416
	IV	248	31,778		IV	246	27,774
Fourchu							
1960	I	479	52,219				
	II	280	44,512				
	III	186	28,953				
	IV	112	23,743				
Gabarus				*Gabarus*			
1957	I	13	1,918	1958	I	467	38,995
	II	449	42,582		II	459	40,555
	III	328	33,646		III	218	27,900
	IV	369	39,589		IV	411	38,712
	V	476	46,418		V	286	36,942
	VI	398	42,713		VI	216	30,133
	VII	184	27,654		VII	210	31,655
	VIII	108	23,278		VIII	162	27,886
	IX	77	14,926		IX	95	16,579
Gabarus				*Gabarus*			
1959	I	287	29,535	1960	I	340	38,708
	II	433	40,144		II	281	35,521
	III	285	32,257		III	212	29,774
	IV	258	29,712		IV	157	23,839
	V	82	14,257		V	140	25,633
	VI	128	19,568		VI	197	35,647
	VII	136	19,560		VII	72	17,663
	VIII	139	18,468		VIII	64	21,198
	IX	74	17,462		IX	52	11,356

Table II — continued

ar	Period	No. landed '00	No. of trap hauls	Year	Period	No. landed '00	No. of trap hauls
minegash				*Miminegash*			
6	I	735	48,647	1947	I	643	43,129
	II	423	47,019		II	402	47,866
	III	235	36,654		III	239	45,031
	IV	358	49,093		IV	176	35,164
	V	136	21,553		V	128	25,549
	VI	134	23,165		VI	55	11,406
	VII	143	22,678		VII	17	3,076
	VIII	81	13,340		VIII	17	2,618
minegash				*Miminegash*			
8	I	885	50,577	1949	I	963	40,451
	II	620	62,647		II	461	31,571
	III	339	45,790		III	274	24,238
	IV	244	31,227		IV	225	27,438
	V	220	33,842		V	136	18,859
	VI	104	14,228		VI	117	16,727
	VII	61	8,850		VII	75	9,722
	VIII	57	8,271		VIII	112	11,835
minegash				*Miminegash*			
0	I	830	43,894	1951	I	860	45,760
	II	558	45,351		II	461	37,448
	III	438	43,829		III	423	41,437
	IV	285	37,030		IV	210	23,298
	V	176	23,711		V	243	28,598
	VI	182	25,330		VI	191	25,157
	VII	125	18,382		VII	128	16,349
	VIII	123	17,082		VIII	106	12,299
minegash				*Miminegash*			
2	I	1,112	48,785	1953	I	923	53,357
	II	507	34,222		II	536	55,844
	III	372	37,942		III	394	55,545
	IV	290	33,670		IV	243	45,811
	V	242	32,746		V	141	29,885
	VI	184	26,268		VI	138	26,970
	VII	195	31,518		VII	107	23,314
	VIII	175	23,977		VIII	85	19,799
minegash				*Miminegash*			
4	I	691	56,597	1955	I	1,213	55,387
	II	329	42,705		II	726	59,492
	III	205	34,218		III	349	37,933
	IV	136	28,415		IV	324	42,563
	V	169	35,261		V	195	24,341
	VI	166	39,421		VI	195	24,724
	VII	114	22,335		VII	117	15,602
	VIII	109	20,998		VIII	160	22,887

TABLE II — continued

Year	Period	No. landed '00	No. of trap hauls	Year	Period	No. landed '00	No. of trap hauls
Miminegash				*Miminegash*			
1956	I	1,205	58,213	1957	I	1,186	66,255
	II	686	64,680		II	627	63,955
	III	468	52,566		III	325	43,939
	IV	439	65,554		IV	341	51,617
	V	294	51,563		V	237	44,760
	VI	149	25,212		VI	192	37,635
	VII	132	19,757		VII	121	24,148
	VIII	135	26,009		VIII	99	13,346
Miminegash							
1958	I	1,541	69,728				
	II	996	66,425				
	III	688	71,624				
	IV	377	54,671				
	V	194	34,008				
	VI	271	51,180				
	VII	155	28,606				
	VIII	122	20,346				
Tignish				*Tignish*			
1951	I	299	18,321	1952	I	630	36,138
	II	1,680	145,253		II	694	38,782
	III	1,725	168,528		III	2,152	164,536
	IV	1,303	106,532		IV	862	71,255
	V	713	78,862		V	740	69,784
	VI	994	145,530		VI	713	74,484
	VII	502	117,863		VII	1,303	116,038
	VIII	473	130,757		VIII	1,402	125,990
	IX	264	34,978		IX	537	61,950
					X	632	87,368
					XI	17	. . .
Tignish				*Tignish*			
1953	I	1,262	133,444	1954	I	510	64,447
	II	996	164,211		II	433	61,954
	III	912	137,805		III	975	158,014
	IV	298	53,997		IV	476	82,275
	V	539	86,742		V	765	145,091
	VI	770	100,639		VI	589	119,533
	VII	516	87,078		VII	766	211,533
	VIII	558	104,416		VIII	673	132,068
	IX	186	68,351		IX	163	45,265
Tignish				*Tignish*			
1955	I	1,445	120,245	1956	I	2,151	118,139
	II	1,109	119,263		II	1,181	87,275
	III	1,159	171,378		III	1,521	117,083
	IV	1,190	121,388		IV	1,054	98,828
	V	492	68,078		V	1,017	118,717
	VI	316	57,950		VI	816	95,500
	VII	743	134,602		VII	1,019	126,205
	VIII	648	116,075		VIII	739	100,167
	IX	454	84,542		IX	695	106,237

TABLE II — continued

ear	Period	No. landed '00	No. of trap hauls	Year	Period	No. landed '00	No. of trap hauls
ignish							
958	I	2,497	134,369				
	II	1,526	113,604				
	III	1,730	222,294				
	IV	1,547	209,304				
	V	568	86,355				
	VI	635	132,028				
	VII	657	157,735				
	VIII	517	145,685				
	IX	165	33,705				
ort Maitland				*Port Maitland*			
947–48	I	428	18,483	1948–49	I	490	22,773
	II	143	6,683		II	223	12,842
	III	149	10,108		III	219	15,938
	IV	47	4,508		IV	170	13,610
	V	62	5,059		V	86	9,736
	VI	2	175		VI	66	7,928
	VII	39	4,874		VII	118	15,188
	VIII	57	7,705		VIII	104	17,245
	IX	167	19,928		IX	390	46,681
	X	471	48,743		X	367	48,237
	XI	494	56,092		XI	260	30,012
	XII	510	54,984		XII	399	55,460
	XIII	378	43,865		XIII	182	30,178
ort Maitland				*Port Maitland*			
949–50	I	636	31,135	1950–51	I	604	33,664
	II	328	20,782		II	495	27,743
	III	233	13,919		III	282	17,254
	IV	93	8,580		IV	207	14,764
	V	115	10,828		V	119	11,190
	VI	91	12,228		VI	156	16,263
	VII	...	...		VII	132	14,757
	VIII	63	9,071		VIII	254	32,922
	IX	144	24,610		IX	299	45,519
	X	399	57,257		X	325	43,523
	XI	430	64,810		XI	247	37,478
	XII	240	38,365		XII	276	43,367
	XIII	268	46,096		XIII	222	37,960
ort Maitland				*Port Maitland*			
953–54	I	323	17,990	1954–55	I	326	23,763
	II	173	11,334		II	137	14,498
	III	202	14,979		III	161	15,653
	IV	155	14,788		IV	109	13,829
	V	61	9,908		V	55	7,776
	VI	58	10,008		VI	33	5,834
	VII	92	13,913		VII	35	6,232
	VIII	77	12,233		VIII	50	8,406
	IX	193	28,768		IX	143	21,494
	X	253	39,207		X	324	49,637
	XI	336	49,257		XI	335	54,674
	XII	286	43,376		XII	270	44,362
	XIII	135	22,518		XIII	126	25,726

TABLE III. Number of lobsters tagged at beginning of season and subsequent returns by periods.

Year	Total tagged	Returns by period													Dates unknown	Period tagging completed
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII		
Fourchu																
1953	998	9	94	152	174	...	...	...	...	...	...	...	...	...	7	I
1954	999	7	153	163	130	...	...	...	...	...	...	...	...	...	–	I
1956	996	33	263	270	149	...	...	...	...	...	...	...	...	...	–	I
1957	1000	10	147	346	118	...	...	...	...	...	...	...	...	...	3	I
1958	1000	48	237	255	154	...	...	...	...	...	...	...	...	...	9	I
1959	1000	43	288	166	139	...	...	...	...	...	...	...	...	...	–	I
1960	999	149	309	180	124	...	...	...	...	...	...	...	...	...	–	I
Gabarus																
1957	1000	0	1	12	19	133	113	82	38	27	...	...	...	...	112	II
1958	1000	5	18	23	101	106	65	100	76	36	...	...	...	...	108	I
1959	1000	0	14	44	69	39	63	49	58	37	...	...	...	...	39	I
1960	997	2	26	74	50	86	150	47	65	35	...	...	...	...	41	I
Miminegash																
1946	1000	372	185	84	64	16	18	9	12	...	...	...	...	...	1	
1947	998	424	253	94	43	13	8	2	4	...	...	...	...	...	3	completed before the beginning of the season
1948	999	450	226	45	57	25	11	5	2	...	...	...	...	...	10	
1949	974	351	145	80	73	30	28	5	3	...	...	...	...	...	9	
1950	1000	276	185	125	34	19	20	13	8	...	...	...	...	...	2	
1951	1000	394	165	87	28	26	16	15	7	...	...	...	...	...	23	
1952	990	289	126	61	58	28	17	6	4	...	...	...	...	...	34	
1953	997	393	202	85	44	19	11	8	5	...	...	...	...	...	25	
1954	996	523	133	56	30	25	21	12	9	...	...	...	...	...	22	
1955	997	426	176	61	52	18	23	7	7	...	...	...	...	...	1	
1956	1000	479	144	66	59	26	14	12	8	...	...	...	...	...	0	
1957	1000	499	142	54	38	21	16	5	0	...	...	...	...	...	44	
1958	999	425	191	112	35	14	7	10	6	...	...	...	...	...	1	
Tignish																
1951	1000	0	22	124	150	65	115	78	60	28	...	...	...	...	2	II
1952	960	0	1	69	49	36	74	109	121	76	33	...	...	...	11	II
1953	999	8	52	83	28	48	79	73	84	69	...	...	...	...	0	I
1954	1000	0	6	50	46	111	88	89	74	31	...	...	...	...	0	II
1955	1000	14	34	75	121	67	35	109	75	56	...	...	...	...	0	I
1956	1000	5	17	61	89	75	102	78	72	66	...	...	...	...	2	I
1958	1000	10	25	78	163	70	66	83	69	16	...	...	...	...	0	I
Port Maitland																
1947–48	1000	145	54	19	4	9	2	5	6	9	15	89	68	33	7	completed before the beginning of the season
1948–49	1000	239	55	36	31	5	4	16	8	24	43	33	56	11	0	
1949–50	1000	159	60	35	18	11	9	0	13	9	25	35	36	92	12	
1950–51	999	75	37	51	12	12	14	9	20	19	30	37	60	44	11	
1953–54	1000	95	28	53	17	7	3	12	30	36	42	34	53	45	2	
1954–55	999	126	40	43	21	3	1	2	1	19	77	63	51	24	3	

TABLE IV. Average temperatures and corresponding activity indices by periods.

	Period	Average temp. (°C)	Activity index		Period	Average temp. (°C)	Activity index
ourchu				*Fourchu*			
53	I	3.8	8.5	1954	I	4.1	9.0
	II	5.8	10.0		II	5.6	10.0
	III	9.2	14.5		III	8.3	13.5
	IV	10.8	17.5		IV	9.6	14.5
ourchu				*Fourchu*			
956	I	1.9	5.0	1957	I	2.2	6.5
	II	3.9	8.5		II	2.8	7.0
	III	6.0	11.0		III	6.9	10.5
	IV	10.0	15.5		IV	7.3	12.5
ourchu				*Fourchu*			
958	I	5.8	10.0	1959	I	2.8	8.0
	II	6.8	11.5		II	5.4	9.5
	III	8.0	13.0		III	6.2	10.5
	IV	11.7	16.0		IV	6.2	11.0
ourchu							
960	I	5.2	10.0				
	II	6.2	11.0				
	III	8.2	14.0				
	IV	9.4	15.0				
abarus				*Gabarus*			
957	I	...	...	1958	I	3.9	8.5
	II	−1.0	1.0		II	3.3	8.0
	III	−0.1	1.5		III	3.7	8.5
	IV	2.4	1.5		IV	6.6	10.5
	V	5.1	9.0		V	7.5	12.0
	VI	6.5	10.0		VI	8.1	13.0
	VII	6.5	10.5		VII	9.3	15.0
	VIII	7.4	13.0		VIII	11.2	17.5
	IX	8.5	14.0		IX	11.5	17.5
abarus				*Gabarus*			
959	I	2.3	7.0	1960	I	3.1	7.5
	II	3.0	7.0		II	5.1	9.5
	III	4.1	8.5		III	4.9	9.5
	IV	4.6	9.0		IV	5.3	10.0
	V	3.3	8.5		V	6.9	12.5
	VI	4.2	9.0		VI	7.8	13.5
	VII	4.2	9.0		VII	7.6	13.5
	VIII	7.0	11.0		VIII	9.1	14.0
	IX	6.6	11.0		IX	8.5	14.5

TABLE IV — continued

	Period	Average temp. (°C)	Activity index		Period	Average temp. (°C)	Activity index
Tignish				*Tignish*			
1951	I	1.7	6.0	1952	I	1.6	5.0
	II	3.0	7.5		II	2.1	7.0
	III	4.9	9.0		III	2.9	8.0
	IV	5.7	9.5		IV	3.4	8.3
	V	5.5	10.0		V	5.9	10.0
	VI	5.4	10.5		VI	5.8	10.5
	VII	7.1	12.5		VII	8.2	12.0
	VIII	10.7	14.0		VIII	10.8	14.5
	IX	13.7	16.4		IX	10.9	15.5
	X	...	...		X	...	...
Tignish				*Tignish*			
1953	I	2.9	7.5	1954	I	2.9	8.0
	II	3.8	8.0		II	2.9	8.0
	III	5.0	9.0		III	3.0	8.0
	IV	6.1	10.5		IV	3.9	9.0
	V	7.1	11.5		V	5.9	10.5
	VI	8.4	11.8		VI	7.3	12.0
	VII	9.7	15.0		VII	8.7	13.5
	VIII	10.4	16.0		VIII	10.2	15.0
	IX	11.0	16.4		IX	11.6	16.4
	X	...	...		X	...	...
Tignish				*Tignish*			
1955	I	4.5	10.0	1956	I	2.6	7.5
	II	3.7	9.0		II	3.0	8.0
	III	4.5	9.5		III	4.2	9.0
	IV	5.6	10.5		IV	5.9	10.0
	V	6.0	11.0		V	6.3	11.0
	VI	6.5	11.8		VI	6.5	11.2
	VII	7.8	13.5		VII	10.0	14.5
	VIII	7.4	13.0		VIII	11.1	16.0
	IX	10.7	15.0		IX	11.3	16.4
	X	...	...		X	...	...
Tignish							
1958	I	3.6	9.0				
	II	3.4	9.0				
	III	5.1	10.0				
	IV	6.8	11.0				
	V	5.3	10.5				
	VI	7.4	12.0				
	VII	9.7	14.0				
	VIII	10.4	15.5				
	IX	11.5	16.4				
	X	...	...				

TABLE IV — continued

	Period	Average temp. (°C)	Activity index		Period	Average temp. (°C)	Activity index
rt Maitland				*Port Maitland*			
47–48	I	4.4	9.5	1948–49	I	8.2	14.0
	II	3.4	8.5		II	6.5	11.5
	III	2.9	8.0		III	4.9	10.0
	IV	...	...		IV	4.2	9.5
	V	1.9	7.0		V	3.8	9.0
	VI	...	...		VI	2.9	8.0
	VII	1.6	6.5		VII	2.3	7.0
	VIII	0.0	6.0		VIII	2.0	7.0
	IX	1.4	6.5		IX	2.2	7.0
	X	2.6	7.0		X	2.6	8.0
	XI	3.9	8.5		XI	4.7	10.0
	XII	4.5	9.0		XII	6.3	11.0
	XIII	...	...		XIII	...	...
ort Maitland				*Port Maitland*			
49–50	I	6.3	11.5	1950–51	I	7.9	14.0
	II	5.1	10.5		II	7.7	14.0
	III	3.8	9.0		III	6.3	12.0
	IV	3.6	9.0		IV	3.5	9.0
	V	2.6	8.0		V	3.1	8.5
	VI	1.9	7.0		VI	2.9	8.0
	VII	...	...		VII	3.1	8.0
	VIII	1.4	6.5		VIII	...	...
	IX	1.3	6.5		IX	3.4	8.5
	X	2.0	7.0		X	3.6	8.5
	XI	3.5	8.5		XI	4.0	9.0
	XII	4.2	9.0		XII	5.9	11.0
	XIII	4.5	9.5		XIII	6.1	11.5
ort Maitland				*Port Maitland*			
53–54	I	9.0	15.0	1954–55	I	6.3	12.0
	II	8.3	14.5		II	6.0	11.5
	III	5.6	11.0		III	5.8	11.5
	IV	4.9	10.5		IV	4.3	9.5
	V	1.5	7.0		V	...	...
	VI	0.6	6.0		VI	0.8	6.0
	VII	1.4	6.5		VII	...	...
	VIII	2.7	8.0		VIII	1.5	6.0
	IX	2.8	8.0		IX	...	...
	X	3.1	8.0		X	4.1	9.0
	XI	4.7	9.0		XI	4.9	9.5
	XII	5.8	11.0		XII	5.8	10.5
	XIII	7.4	12.5		XIII	7.2	12.0

Let t_o denote the first period when the tagged lobsters are considered to have had sufficient time to mix with the resident population. The population size at the start of the period t_o has then been estimated from:

$$N_{t_o} = \frac{X_{t_o}\,(K_{k+1} - K_{t_o})}{\sum\limits_{t_o}^{k} x_i} \tag{1}$$

To obtain N_1 (the population size at the beginning of the season), we have simply added the accumulated catch K_{t_o} to N_{t_o}, i.e.,

$$N_1 = N_{t_o} + K_{t_o} \tag{2}$$

Formula (1) can be considered as having been obtained in two different ways. First of all, it is a maximum likelihood estimate in a hypergeometric sampling scheme (binomial sampling without replacement (Chapman, 1948)). Secondly, we can get the estimate (1) by the least squares method.

Following DeLury (1958) and using the least squares method, we choose N_{t_o} so as to minimize

$$\sum_{t = t_o}^{k} w_t \left(\frac{x_t}{C_t} - \frac{X_t}{N_1 - K_t}\right)^2 \tag{3}$$

where w_t's are appropriate weights, customarily taken to be proportional to the inverse of the variance of x_t/C_t. When the tagged and untagged lobsters are randomly mixed, these variances may be calculated by assuming Poisson or binomial sampling. It will be shown later that in our data x_t/C_t varies more than expected on the basis of random fluctuations. Under these circumstances DeLury argues that one should preferably take $w_t = C_t$.

To arrive now at a simple formula for the population size we substitute $w_t = C_t$ and the approximate identity

$$\frac{X_t}{N_1 - K_t} \sim \frac{X_{t_o}}{N_{t_o}} \tag{4}$$

in (3); approximation (4) follows from the fact that the tagged and untagged lobsters are (assumed to be) removed at the same rate. When (3) (with (4) substituted in it) is minimized with respect to N_{t_o} we get an estimate for N_{t_o} as in (1).

Approximate confidence limits for $1/N_{t_o}$ may be calculated by standard regression techniques. These limits may then be inverted to arrive at estimates of the limits $(N_{t_o}, \overline{N}_{t_o})$ for N_{t_o}. The procedure leads to the following formula for the 100 $(1 - \alpha)$ % confidence limits

$$(N_{t_o}, \overline{N}_{t_o}) = \frac{X_{t_o}\,(K_{k+1} - K_{t_o})}{\Sigma x_t \pm t\alpha s \sqrt{K_{k+1} - K_{t_o}}} \tag{5}$$

where $t\alpha$ is Student's t-value with $k - t_o - 1$ degrees of freedom and s is calculated from

$$\Sigma\, C_t \left(\frac{x_t}{C_t} - \frac{X_{t_o}}{N_{t_o}}\right)^2 = (k - t_o - 1)s^2 \tag{6}$$

TE OF EXPLOITATION

The rate of exploitation may be calculated from

$$u = \frac{K_{k+1}}{N_1}$$

d limits for u may be obtained by replacing N_1 by $\overline{N}_{t_o} + K_{t_o}$ and $N_{t_o} + K_{t_o}$ rmula (5)). Other authors (Ricker, 1958) have suggested use of Poisson its. One suspects, however, that the Poisson limits would be far too narrow the variability in data exceeds that predicted from the Poisson distribution of returns.

TCHABILITY OF LOBSTERS

The probability that a lobster will be captured by a randomly applied unit effort is called the catchability coefficient. It is denoted here by q. If the mbers caught by one unit of effort follow a Poisson distribution, we get an proximate relationship between the catch and number of effort units applied

$$C_t = N_t\,(1 - e^{-qf}t)$$

is is the familiar catch equation dating back to Nicholson and Bailey (1935) d used extensively, with some minor variation, in many fisheries studies.

In (8) the catchability coefficient q is assumed to be independent of the pulation size and effort. To study the variations in q in time (8) may be itten in the form:

$$q_t = -\left\{\log_e\left(1 - \frac{C_t}{N_t}\right)\right\}/f_t$$

$$q_t = \left\{\log_e \frac{N_t}{N_{t+1}}\right\}/f_t$$

the values of N_t are known, say from the tagging studies, the weekly values q_t may be estimated. The tag returns may also be used directly in evaluating s. The corresponding formula is then:

$$)\qquad q_t = \left\{\log_e \frac{X_t}{X_{t+1}}\right\}/f_t$$

On the basis of experimental studies (McLeese and Wilder, 1958) q_t is ected to be related to water temperature c_t^o through

$$)\qquad q_t = q(c_t^o - c_o)$$

ere c_o is the temperature at which the lobsters become inactive.

As the catch of lobsters by traps is dependent on their activity, one may te analogous to (11)

$$)\qquad q_t = q(a_t - a_o)$$

ere a_t is now the index of activity (walking rate) at the temperature to which lobsters are acclimated during the period t.

For the formulae (11) and (12) to be comparable, the activity indices must inearly related to temperatures. For the range of temperature we are working with, this actually is the case (McLeese and Wilder, 1958). When temperatures are above the range where the linear relationship between temperature and the index of activity breaks down, the catchability correction would have to be based on the index of activity rather than temperature.

POPULATION SIZE ESTIMATES FROM CATCH AND CATCH-PER-EFFORT DATA

Leslie and Davis (1939) and DeLury (1947, 1951) have developed a method of estimating the size of a closed exploited population. Their method makes use of the gradual decline in the catch per unit of effort plotted against accumulated catch. The equations, given by Leslie and Davis and DeLury, assume constant catchability; their equations can, however, be easily modified to take account of varying catchability. Thus, assuming that q_t is given by (11), the relationship between the catch per unit of effort and the accumulated catch, proposed by Leslie and Davis and DeLury, may now be rewritten:

$$(C/f)_t = q(c_t^{\circ} - c_o)\ (N_1 - K_t) \tag{13}$$

If indices of activity are used, equation (13) becomes:

$$(C/f)_t = q(a_t - a_o)\ (N_1 - K_t) \tag{14}$$

The values q, c_o, and N_1 in (13), or q, a_o and N_1 in (14) (note that q in (13) does not necessarily equal q in (14)) are unknown and must be estimated. However, they cannot be estimated by standard regression or least squares techniques. First of all, the above equations are not linear in q, c_o (a_o), and N_1, and secondly the coefficients of these unknowns, namely c_t° or a_t are not free of error.

To estimate q, c_o and N_1 from catch, catch–per–effort and temperature data, we assume that we have approximate solutions say, q', c_o' and N_1' at our disposal. These may have been obtained from the tagging and catch data or from (13) by putting $c_o = 0$ and estimating q' and N_1' by regression techniques (DeLury, 1951). Let the corrections to the approximate solutions be Δq, Δc_o, and ΔN, i.e.,

$$\begin{aligned} q &= q' + \Delta q \\ c_o &= c_o' + \Delta c_o \\ N_1 &= N_1' + \Delta N \end{aligned} \tag{15}$$

Denote further

$$F_{ot} = (C/f)_t - q'\ (c_t^{\circ} - c_o')\ (N_1' - K_t) \tag{16}$$

i.e., F_{ot} is the difference between $(C/f)_t$ and its estimate (13) when the approximate values of q, c_o and N_1 are used.

By ignoring all the correction terms of the second or higher order we get

$$\begin{aligned} F_t \sim F_{ot} &- [(c_t^{\circ} - c_o')\ (N_1' - K_t)]\Delta q \\ &+ [q'\ (N_1' - K_t)]\ \Delta c_o - [q'\ (c_t^{\circ} - c_o')]\Delta N \end{aligned} \tag{17}$$

where we have denoted

$$F_t = (C/f)_t - q(c_t^{\circ} - c_o)\ (N_1 - K_t)$$

The equation (17) is now linear in the unknowns Δq, Δc_o, and ΔN. In ctice perhaps not too great an error would be committed if the unknowns were mated by regression techniques. Since, however, the coefficients of Δq, Δc_o l of ΔN are all subject to error, we would prefer non-parametric methods.

Trial fittings of parameters in (17) have shown that estimation of annual ue of Δq and Δc_o is not warranted. Hence only an estimate of average q and over all years has been attempted. To present the appropriate equations en all the years for each area are considered together, we rewrite (17) and roduce the index i to denote the year

′)

$$F_{ti} \sim F_{oti} - G_{ti}\Delta q + L_{ti}\Delta c_o - M_{ti}\Delta N_i$$

ere

)

$$G_{ti} = (c^o_{ti} - c'_o)\ (N'_i - K_{ti})$$
$$L_{ti} = q'\ (N'_i - K_{ti})$$
$$M_{ti} = q'\ (c^o_{ti} - c'_o)$$

l c^o_{ti} = average temperature during the t^{th} period in the year i, etc.

Suppose i (the year) runs from i = 1, . . . , r. Then we have rk equations of e (17′) (r years, k periods in each). To estimate Δq, Δc_o and the ΔN_i's we ve simply added different combinations of equations (17′) to arrive at r + 2 new ations (r + 2 = number of unknowns Δq, Δc_o, and ΔN_i, i = 1,...r). This proce-e may be compared with the commonly used method of estimating parameters h the aid of investigational variables (Reiersol, 1945) and also with the method itting a straight line by grouping the observations (Wald, 1940). Note that the uping is independent of observation errors (Neyman and Scott, 1951) since may group (17′) by periods.

Assume for instance that there are 4 periods (i.e., k = 4) and 7 years (i.e., 7) (Fourchu). Then we may take as the equations determining the unknowns following 9 equations:

$$\sum_{t=1}^{4} F_{ti} = 0 \quad i = 1, \ldots, 7$$

)

$$\sum_{i=1}^{7} F_{1i} = 0$$

$$\sum_{i=1}^{7} F_{4i} = 0$$

ere F_{ti}'s are given by (17′) and (18).

To some extent the manner of arriving at equations (19) is arbitrary. ferent grouping of equations (17′) would have given a system differing from) and, no doubt, would have led, when solved, to somewhat different values the correction terms Δq, Δc_o and ΔN_i. This arbitrariness cannot be avoided e very little is known about errors in our observational data.

The method for calculating confidence limits for the estimates from (19) not been worked out.

ANALYSIS OF DATA

TAGGING-RECAPTURE DATA

Tagging and catch data provide a means of directly estimating rate of exploitation, population size, and catchabilities of lobsters, provided that the tagged and untagged lobsters are randomly mixed, equally catchable and that the fishermen report the recaptured lobsters promptly. To estimate the population size, the population should be a closed one. These assumptions can be checked only indirectly in our data.

If the catchability of tagged and untagged lobsters is the same, and if there is no immigration into the study area from outside, the catch of tagged and untagged lobsters should follow the same trend, i.e., the ratio

$$x_t/C_t$$

should be more or less constant, apart from random fluctuations. The magnitude of the latter can be easily assessed, under the assumption of perfect (random) mixing, by using a normal approximation to the Poisson distribution with the (approximate) mean = x_t/C_t. For example, in the Tignish area in 1958, $x_4/C_4 = .105 \times 10^{-4}$. The approximate 95% confidence limits for the corresponding population parameter are $.089 \times 10^{-4}$, $.122 \times 10^{-4}$. The width of this confidence interval is small compared with the observed fluctuations in the ratio x_t/C_t (cf. Fig. 1).

If the weekly values of x_t/C_t fluctuate more than predicted by the Poisson distribution (as they do) perfectly random mixing has not been realized. This does not necessarily mean that population size estimates based on tag returns are not valid, but only that confidence limits for the population size estimates will be wider than those based on Poisson, binomial or hypergeometric limits.

Our main concern is whether or not there are any trends in the graph of x_t/C_t values plotted against time. These graphs for the five study areas are given in Fig. 1. Panel A denotes the plots for the cold water areas (Fourchu, Gabarus, Tignish) where the temperature is increasing as the season progresses; Panel B for a warm water area (Miminegash) with relatively stable temperature; Panel C depicts the plot for a relatively cold water area (Port Maitland) with both decreasing and increasing water temperature trends present. In all the graphs definite trends in the x_t/C_t values can be detected. In Panel A the catchability of tagged lobsters, compared with the untagged lobsters, is increasing; in Panels B and C the trend is opposite. It is apparent that, where temperature trends are present at the beginning of the season, relative catchability of tagged lobsters (i.e., ratio of tagged to untagged) follows the same pattern as the temperature in our study areas, although judging from the fact that there are trends observed in the Miminegash data, other factors must be affecting the relative catchability as well.

We suspect that the observed trends in the x_t/C_t values are attributable to the difference found between the cold and warm water areas in the initial distributions of tagged and untagged lobsters. This will be considered in a later section (distribution of tagged versus untagged lobsters).

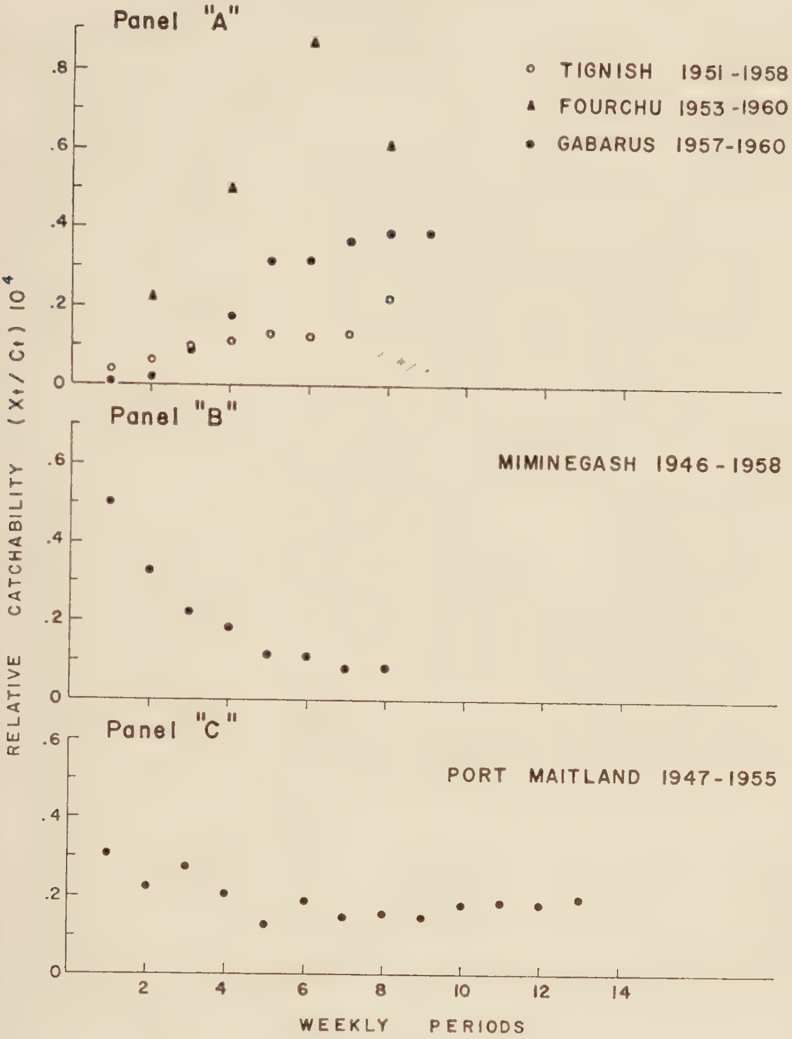

FIG. 1. Relative catchability of tagged lobsters.

ULATION SIZE ESTIMATES

Differences in the behaviour of tagged and untagged lobsters affect the ulation size estimates. It is not obvious whether these differences will result n over- or under-estimate of the population size. For instance, one might k that a low relative catchability at the start of the season would imply that average catchability of the tagged lobsters for the season would be lower than of the untagged ones and correspondingly that the population size would be -estimated by the tagging-recapture method. On the other hand, however, ow catchability at the start of the season in areas such as Fourchu, Gabarus Tignish means that more tagged lobsters are on the ground toward the latter part of the season when the water is warm and when the over-all catchability is much higher. Thus the upward trend in water temperatures would tend to result later on in a partial compensation for the initially low relative catchability of tagged lobsters.

In Table V, the estimated population sizes at the beginning and at the end of the season are given for all the areas except Miminegash. For the Miminegash area, only the first four periods can be considered because some moulting, with attendant loss of tags and increase in population size of legal-size lobsters due to growth of sub-legals to legals, takes place beginning about the fourth or fifth week; the population size estimates are therefore at the start of the first and fifth period (week).

Formulae (1) and (2) have been employed to arrive at estimates of the population sizes at the start of the season. The confidence limits are obtained from (5). Estimates of population remaining at the end of the season are obtained by subtracting the total catch per season from N_1.

RATE OF EXPLOITATION

The population size estimates can be used to obtain estimates of the rates of exploitation (formula (7)). These are included in Table V and will be used later in interpreting the differences in expression of trends in the catchability.

From the limits for the population size estimates, we can calculate the limits for the rate of exploitation (cf. formula (7) and subsequent explanation). For instance for Tignish, 1954, we get from Table V $\mu = .58$ with limits .51 to .63. The Poisson limits calculated first for N_{t_0} and then for N_1 as before would be from .53 to .62, in this case only slightly narrower than the regression limits.

CATCHABILITIES

Catchabilities have been calculated from the population size estimates and the observed catches (formula (9)) or from the estimated number of tags in the water (formula (10)). While in the first method the population size estimates also depend on the tag returns, the catchabilities calculated in those two ways are to some extent independent. That is, catchabilities, q_t, calculated from the population size estimates depend only on the total tag returns for the season; they follow closely the fluctuations in total catches. On the other hand, catchabilities calculated from the tag returns, denoted now by q'_t to distinguish it from q_t above, follow the rate of recapturing the tagged lobsters.

To exhibit the dependence of catchability on temperature and on activity, correlation coefficients have been calculated between their respective values except at Miminegash where there is little change in temperature during the season. For each other area and year, we have four correlation coefficients: between q_t and c_t^o, q_t, and a_t, q'_t and c_t^o, and q'_t and a_t. The results are tabulated in Table VI.

We note first of all from Table VI that there is little difference in the correlation coefficients between q_t and c_t^o and between q_t and a_t on the one hand and between q'_t and c_t^o and between q' and a_t on the other. This is easily understandable since, within the range of temperatures covered, the index of activity is

TABLE V. Estimated population sizes at the start and at the end of the season and confidence limits for the population size estimates at the start of the season.

A. Population size estimates based on tagging-recapture and catch data.

Area and year	At start of season	Limits at start		At end of season	Rate of exploitation
	'00	'00		'00	
Fourchu					
1953	1,635	862	21,466	914	.44
1954	1,770	1,501	2,166	925	.48
1956	1,849	1,731	1,988	455	.75
1957	1,844	1,193	4,735	638	.65
1958	1,683	1,383	2,245	402	.76
1959	1,785	1,128	37,785	510	.71
1960	1,281	1,156	1,463	224	.83
Gabarus					
1950	3,633	2,960	4,968	1,397	.62
1956	5,127	4,244	6,752	1,954	.62
1957	3,833	2,751	7,581	1,431	.63
1958	3,382	2,880	4,294	858	.75
1959	3,197	2,724	4,033	1,376	.57
1960	2,128	1,778	2,892	614	.71
*Miminegash**					
1946	2,481	1,585	5,706	730	.71
1947	1,781	1,151	3,948	323	.82
1948	2,648	1,570	8,455	561	.79
1949	2,850	2,468	3,371	927	.67
1950	3,394	2,347	6,130	1,283	.62
1951	2,811	1,710	7,905	858	.69
1952	3,997	3,666	4,393	1,717	.57
1953	2,797	1,846	5,772	701	.75
1954	1,779	1,017	7,090	418	.77
1955	3,638	2,397	7,540	1,026	.72
1956	3,740	2,078	18,666	942	.75
1957	3,199	1,802	14,199	720	.77
1958	4,712	3,071	10,120	1,109	.76
Port Maitland					
1947–48	7,191	5,097	12,681	4,244	.41
1948–49	5,481	3,682	10,723	2,406	.56
1949–50	5,916	4,379	9,115	2,876	.51
1950–51	8,388	6,586	11,544	4,771	.43
1953–54	5,129	4,041	7,018	2,786	.46
1954–55	4,436	3,525	5,977	2,332	.47
Tignish					
1951	10,994	9,928	12,501	3,041	.72
1952	13,897	11,187	19,545	4,215	.70
1953	9,611	7,243	18,559	3,574	.63
1954	9,298	8,437	10,421	3,948	.58
1955	10,992	9,972	12,409	3,436	.69
1956	14,968	13,174	17,747	4,775	.68
1958	13,520	12,684	14,584	3,678	.73

B. Population size estimates based on catch-effort-temperature data.

Area and year	At start of season
Fourchu	'00
1953	2105
1954	1928
1956	2044
1957	1873
1958	1961
1959	1860
1960	1311

*Figures are for the start of the season and the start of the fifth week.

TABLE VI. Correlation coefficients between catchability and temperature and between catchability and activity.

	Correlation coefficients			
	Based on tag returns		Based on population size estimates	
	$r_{q_t\theta_t^0}$	$r_{q_t a_t}$	$r_{q'_t\theta_t^0}$	$r_{q'_t a_t}$
Fourchu				
1953	.985	.996	.920	.884
1954	.974	.993	.941	.944
1956	.917	.923	.971	.984
1957	.969	.999	.982	.997
1958	.651	.721	.965	.979
1959	.993	.902	.601	.721
1960	.991	.962	.986	.994
Av. all years combined:	.927	.928	.958	.972
Gabarus				
1957	.864	.869	.546	.466
1958	.973	.962	.919	.892
1959	.629	.779	.380	.782
1960	.928	.948	.417	.512
Av. all years combined:	.900	.924	.641	.711
Port Maitland				
1947–48	.531	.696	.661	.778
1948–49	.825	.860	.808	.601
1949–50	.834	.854	.776	.815
1950–51	.702	.680	.592	.641
1953–54	.757	.771	.886	.913
1954–55	.700	.789	.721	.794
Av. all years combined:	.740	.782	.758	.763
Tignish				
1951	.467	.390	.401	.315
1952	.830	.900	.760	.721
1953	.942	.906	.507	.414
1954	.712	.697	.394	.408
1955	.589	.529	.575	.527
1956	.355	.380	.277	.309
1958	.067	.166	−.428	−.358
Av. all years combined:	.653	.647	.390	.359

rly related to temperature. However, since the acclimation states of lobsters which the index of activity is based) do not respond quickly to small temper- e changes, it was anticipated that the use of the indices of activity would ide a convenient way of smoothing the temperature data. The smoothing not, however, make any significant improvement in the catchability–temper- e correlation. For this reason we deal in the remaining part of this account ly with the temperature data. In some other studies where the temperature surements vary more widely and the indices of activity can be determined accurately, it may be more appropriate to correlate the index of activity catchability.

The correlation coefficients listed in Table VI were tested for homogeneity een years within each of the areas. The results showed no significant rtures from homogeneity; hence, we combined all years to give one combined elation coefficient for each area and pair of variates, q_t and c_t°, etc. The -all correlation coefficients were obtained by transforming the r's before ng the average and then retransforming the average back to an "r" in the l fashion (cf. Rider, 1947). The resulting r's are all significant at the 5% l. In the Fourchu area the combined correlation coefficients based on tag

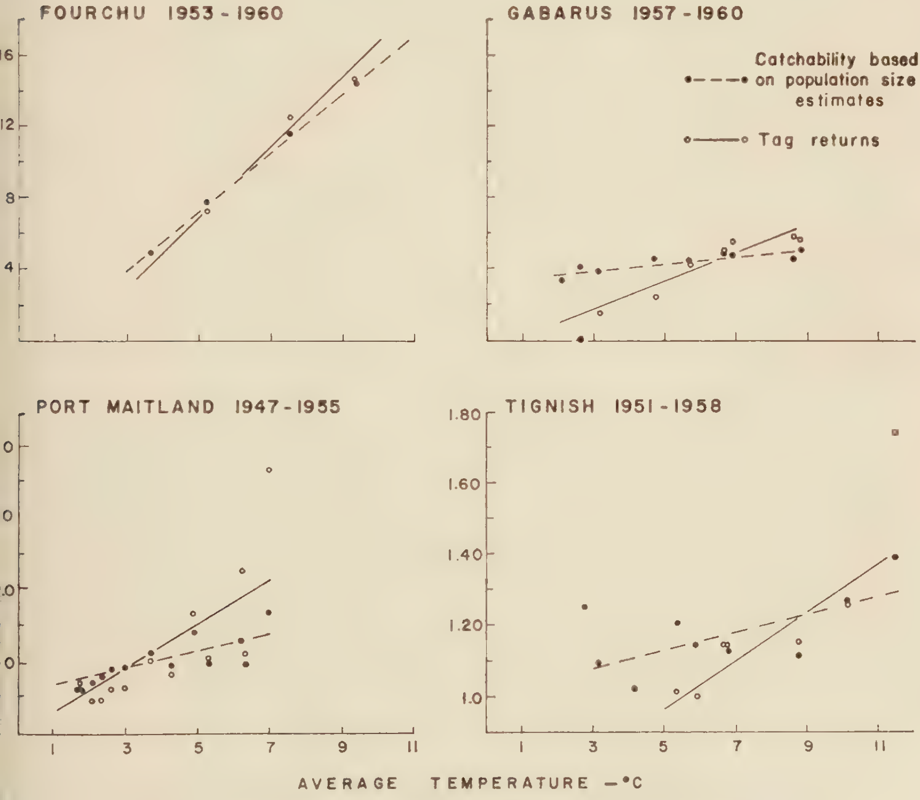

FIG. 2. Relationship between catchability and temperature.

returns are simply averages over all years since the above calculations could not be made with only three degrees of freedom available for each year.

Correlations between the catchabilities and temperatures are presented in graphic form in Fig. 2. Each point in the graphs represents an average catchability (q_t or q'_t) for one period calculated over all the years studied.

A straight line $q_t = q(c_t - c_o)$ or $q'_t = q'(c^o_t - c')$ has been drawn through the points in each graph in Fig. 2. The numerical values for q and c_o and for q' and c'_o as well as for a_o and a'_o are given in Table VII. The lines were fitted by simply dividing the periods into two groups, calculating the average x and y co-ordinates for those groups and fitting a line through the two points obtained. The periods were grouped retaining their time sequence except in the case of Port Maitland. If the number of periods for which data are available was even, the first half of the periods was taken in the first group and the others in the second. In the case of an uneven number of periods, the middle period has been left out. In effect, this procedure resulted in grouping the periods with low and high average temperatures respectively. To obtain similar grouping for Port Maitland, the periods 1, 2, 3, 11, 12 and 13 were included in the first group, and the remainder in the second. The approximate confidence limits for q and q′ were determined by a method developed by Bartlett (1949) (cf. also Madansky, 1959, page 185 for a correction). These limits were calculated only for catchability coefficients based on temperature data. They are included in Table VII.

TABLE VII. Coefficients for equations (11) and (12) expressing numerical relationship between temperature and catchability, and activity and catchability.

Calculated from	Based on	Area			
		Fourchu	Gabarus	Port Maitland	Tignish
Catch and tag returns	temperature	$q = 1.82 \times 10^{-6}$	$.76 \times 10^{-6}$	$.61 \times 10^{-6}$	$.08 \times 10^{-6}$
		$\sigma_q = .30 \times 10^{-6}$	$.37 \times 10^{-6}$	$.22 \times 10^{-6}$	$.03 \times 10^{-6}$
		$c_o = 1.26$	.59	−.12	−6.37
	activity	$q = 1.50 \times 10^{-6}$	$.52 \times 10^{-6}$	$.60 \times 10^{-6}$	.08
		$a_o = 4.86$	−18.17	−4.32	−54.75
Catch and population size estimates based on tag	temperature	$q = 1.67 \times 10^{-6}$	$.18 \times 10^{-6}$	$.23 \times 10^{-6}$	$.016 \times 10^{-6}$
		$\sigma_q = .31 \times 10^{-6}$	$.06 \times 10^{-6}$	.05	$.014 \times 10^{-6}$
		$c_o = .59$	−18.38	−4.72	−68.56
returns	activity	$q = 1.43 \times 10^{-6}$	$.14 \times 10^{-6}$	$.23 \times 10^{-6}$	$.016 \times 10^{-9}$
		$a_o = 4.41$	−21.66	−.34	−62.92
Catch and population size estimates based on catch-per-effort and temperature data		$q = 1.65 \times 10^{-6}$ $c_o = .74$			

The relationships between catchability and temperature and between catchability and the index of activity tabulated in Table VII are not directly ıparable with the results of McLeese and Wilder (1958). They plotted, ead of the estimated catchability as we have done, the catch per 100 trap ls against temperature and against the index of activity. Catch per trap l figures are, at any level of temperature, dependent on the population size. wever, if their catch per trap haul on temperature or the catch per trap haul index of activity lines are extrapolated to zero catch per trap haul, the esponding temperature or index of activity intercept is an estimate of the el at which the activity of lobsters is so low that they are uncatchable, i.e., chability is 0. This level is denoted here by c_0 or a_0. McLeese and Wilder nd c_0 to be about 3°C and a_0 to be about 8 feet per minute, but suggested that se figures might be too high. Their figures can be compared with c_0's and in Table VII.

The values of c_0 and a_0 found from the tagging-recapture data and from the ulation size (i.e., tagging-recapture-catch) data in our study areas differ siderably from the values $c_0 \sim 3$°C and $a_0 \sim 8$ feet per minute. In all of the cases ed, c_0 and a_0 are less than 3°C and 8 feet per minute respectively, in some cases te considerably.

We suspect that the experimentally established values of $c_0 \sim 3$°C and $a_0 = 8$ per minute are too high to be representative of commercial-sized populations. ese values were based on a small population, the density of which was rather compared with the densities we are dealing with. Now, the relationships $= q(c_t^0 - c_0)$ and $q_t = q(a_t - a_0)$ are thought to describe the average behaviour obsters. But at low temperatures, when only a part of the population will be ve, the catch is based on that part of the population and these relationships not hold any more. In small populations this residual would be small since the probability of catching any lobsters under these circumstances is espondingly low, they will not have significant effect on the estimated tionship. Thus we would get different estimates for c_0 and a_0 at different ulation densities by the methods used here. In particular, the higher the sity, the lower the values of c_0 and a_0 would be. Moreover, the lower values $_0$ and a_0 would also result in lower values of q. Concentrations of lobsters, shed selectively, would have an additional effect of lowering the estimated ıes of c_0 and a_0.

In our study areas the tagged lobsters are a small part of the resident popu- on; the populations of tagged lobsters are comparable in size with the experi- ıtal population of McLeese and Wilder and therefore they should be subject he type of density effect discussed in the previous paragraph. Thus we should ect that the values of c_0 and a_0 based on tagging data would be closer to the erimentally established values than those based on the population size mates as indeed they are in the Gabarus, Port Maitland and Tignish areas.

The Fourchu area is an exception to the above. In that area the estimates ained by the two different methods are fairly close, the differences being not ificant. The values of c_0 and a_0 (as well as of c_0' and a_0') in the Fourchu ı are also closer to the values found by McLeese and Wilder than in other areas. In the light of the previous comments this could mean a lack of marked concentrations of lobsters in that area.

While it appears that the markedly different densities of tagged and untagged lobsters should result in the different values of q and q', c_0 and c_0', and a_0 and a_0', some of the observed differences are fairly large, too large to be explained as density effects. We believe that differential distribution of the tagged and untagged lobsters is responsible for most of the discrepancies found. This will be considered in the next section.

Distribution of Tagged Versus Untagged Lobsters

Differences between the catchabilities of the tagged and untagged animals such as are shown for lobsters in the previous section or earlier by changes in the ratio x_t/C_t are commonly met in tagging studies. These discrepancies are usually attributed to the effect of tagging on the animals and on their behaviour. From our general knowledge of lobster populations we believe, however, that differences between the tagged and untagged lobsters are results of the differences in their relative densities on the ground and differences in their initial distributions at the start of the season.

The tagged lobsters when released are distributed more or less uniformly over the study area. General observations on lobsters indicate that the resident population on the other hand would be more concentrated on ledges and on rocky parts of the bottom close to their potential hiding places. This seems to be especially true when the water is cold and less so when the water is warm and lobsters are more active (Wilder, personal communication). Thus the differences between the uniform distribution of tagged lobsters and the non-uniform distribution of the resident population at the start of the season would be more pronounced in the cold than warm-water areas. These differences will presumably disappear at the rate at which the tagged lobsters establish themselves on the bottom. In marking[2] studies (Wilder, personal communication) no indication of the differences has been found in the distribution of marked and unmarked lobsters after the lapse of a year from marking. However, in a short-term study such as this, the initial differences may have serious effect.

In the cold-water areas (Panel A, Fig. 1) fishing at the start of the season is supposedly concentrated on rocky parts of the bottom where most of the lobsters are found. Due to the initially uniform distribution of tagged lobsters, the ratio x_t/C_t would be low in those areas. However, as the season progresses the tagged lobsters have more chance to mix with the resident population resulting in an upward trend in their relative catchability and hence in the ratio x_t/C_t as was actually observed in the graphs in Panel A. The rate at which the relative catchability of tagged lobsters increases is accelerated by the warming of the water with resultant increase in the activity of all lobsters and the tendency to greater dispersal of fishing gear as the initial concentration of lobsters is reduced by fishing.

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[2] Marks (holes punched through the tail) are visible on lobsters for more than a year (Wilder and Murray, 1956). Tags stay on usually only one season as they are cast off in moulting.

In warm-water areas the reverse may be true. The lobsters are more iformly distributed (but not necessarily as uniformly as the newly introduced ged lobsters). Because the lobsters are active there is less reason for fishermen search for areas of concentration and the gear is more evenly spread out proximating the initial distribution of tagged lobsters. This results in a h initial catchability of tagged lobsters which would gradually decrease as the mbers of tagged lobsters are reduced by heavy fishing. Such effects would plain the situation observed in Panel B and Panel C for the first part of the son.

Over and above the main trends in x_t/C_t a number of irregular deviations n be found in graphs in Fig. 1. These we have not considered as having y general significance but rather as peculiar to the particular study area. r example, in Port Maitland during a period in the middle of the season (mid nuary to mid March) the relative catchability of tagged lobsters is rather low. this period only a few lobster traps in deep water are fished because of the d weather and generally low catches. Thus it is likely that the ratio x_t/C_t viates during the midwinter from its average level on account of small sample tch) size alone. In Miminegash some of the irregularities in the graph of C_t plotted against time (Panel B) are due to recruitment to the legal sizes moulting and growth of sub-legal lobsters beginning in the middle of the ason. It may also be that some immigration to the study areas, prompted by pletion of stock by the fishery, takes place during the season.

pulation Size Estimates Based on Catch and Catch-Per-Effort Data

When the population size is estimated from the gradual decline in the tch-per-effort figures as a result of the depletion of stock by fishing, catchability rrected for temperature, in our case q in $q_t = q(c_t^o - c_o)$, should be constant. marked concentrations of lobsters are present, this assumption breaks down. all our areas we have some evidence of the presence of such concentrations cept perhaps in Fourchu where the fact that the estimated values of q and were nearly the same was interpreted as possible evidence of the marked ncentrations. For this reason the population sizes in the Fourchu area only ve been calculated by the catch-per-effort method, i.e., by using equation (18). e initial values for N_{1i} are obtained from Table V and for q and c_o from Table I (tagging-catch data estimates, $q = 1.665 \bullet 10^{-6}$, $c_o = .58$).

The first step in estimating the q, c_o, and the N_{1i} (i stands for the year) the catch, catch-per-effort method is to calculate the catch per trap haul $/f)_t$ for each period and season. Next we substitute the initial values of q, and N_{1i} in (16) to arrive at F_{ot}. For instance, for the first period, 1953, we get:

$$F_{o1} = (C/f)_1 - q(c_t^o - c_o)\ (N_{1i} - C_1) \quad (C_1 = 0)$$

$$= \frac{2663}{12890} - 1.665\ (3.8 - 0.58)\ 163540 \times 10^{-6}$$

$$= -0.6700$$

Similarly we calculate the values of K_{ti}, L_{ti}, M_{ti} (where i now stands for the ear). The final equations (19) are given in Table VIII.

TABLE VIII. Coefficients of equations (19) for Fourchu Area leading to estimates of q, c_o and N_{1i} (population size) based on catch, effort and temperature data.

			$\Delta N_i \times 10^{-8}$							
	Δq	$-\Delta c$	i = 1951	1952	1953	1954	1955	1956	1958	
1	3,719,211	958,774	4542	0	0	0	0	0	0	−2.3241
2	3,582,361	999,212	0	4209	0	0	0	0	0	−0.8596
3	2,041,908	873,835	0	0	3243	0	0	0	0	+0.4719
4	2,056,156	942,956	0	0	0	2811	0	0	0	−0.0883
5	3,122,355	764,508	0	0	0	0	4991	0	0	−1.5372
6	1,968,614	794,546	0	0	0	0	0	3045	0	+0.0795
7	1,736,762	489,697	0	0	0	0	0	0	4443	−0.2302
8	5,927,237	1,972,810	536	586	220	270	896	370	769	−0.9032
9	8,088,742	923,575	1702	1502	1568	1119	1851	936	1469	−1.4201

These equations when solved lead to estimates of q, c_o and N_{1i} for the years (i) considered. The values of q and c_o are included in Table VII and of N_{1i}'s in Table VI. The values arrived at are comparable with the previous estimates in Table VI.

We conclude that the catch, catch-per-effort method when modified to take into account the possibly variable catchability may be used successfully to estimate population sizes when animals are not markedly aggregated. But even when they are, the method would still probably give a rough approximation of the actual population size.

COMPARISON BETWEEN THE AREAS

Discrepancies between tagged and untagged lobsters are possibly, as suggested earlier, in part due to the differences in their distributions. The tagged lobsters are distributed, at least initially, uniformly over the study areas while the resident population may be contagiously distributed. Very little is actually known about the distribution of the lobsters on the bottom. To compare the catchabilities in the different areas we are, therefore, well advised to compare the catchabilities of tagged lobsters, the initial distributions of which are comparable in all our study areas.

Estimated catchabilities at various temperatures for the five study areas are set out in Table IX. They are calculated from tag returns by using the relationship $q_t = q(c_t^o - c_o)$ (Table VII) and interpolated to 5°C, 10°C and to 14.3°C for Fourchu, Gabarus, Port Maitland and Tignish areas. The highest temperature chosen (14.3°C) is the mean temperature during the first 4 weeks of the season in Miminegash. This temperature has been chosen so that the mean catchability at Miminegash may be compared with the extrapolated catchabilities in the other areas.

In Table IX we have also given the average annual numbers of trap hauls per day fished per square nautical mile of lobster grounds and the average temperatures. The average temperatures are obtained by weighting the temperatures for each period and season by the average number of trap hauls by

Table IX. Comparison of catchabilities in the study areas as calculated from tag returns.

	$10^6 q_t$ at			Av. no. of trap hauls per day fished per square nautical mile	Av. water temperature (°C)
	5°C	10°C	14.3°C		
Fourchu	6.8	15.9	23.7	163	6.1
Gabarus	3.4	7.2	10.4	351	5.2
Port Maitland	3.1	6.2	8.9	127	4.2
Tignish	.9	1.3	1.7	555	6.2
Miminegash	...	...	6.8	391	14.3

ods over all the years employed. We note that the catchability figures in le IX are perhaps most reliable in the neighbourhood of the average temperes for the area. The further the temperatures corresponding to the interted catchabilities are from the average for the area, the less likely that the nated catchabilities are reliable.

It is a striking aspect of Table IX that estimated catchabilities differ kedly from area to area. Thus the catchabilities at Fourchu are about t times higher than those in Tignish at 5° and the differences are even greater igher temperatures. While some of the differences between these regions be related to differences in character of the bottom, size of lobsters, etc., it is lly to be expected that the catchability of lobsters would differ so much een areas on those accounts alone.

The widely observed differences in the estimated catchabilities raise the stion of how reliable our estimates are. Examination of Table IX shows , apart from Port Maitland, the order of catchabilities is in reverse to the r of the number of trap hauls per day per area fished. The low number of hauls per day in Port Maitland is due to a long period in the middle of the on when only a few traps are being fished. During the part of the season n most of the lobsters are caught, the number of trap hauls per day is much er (cf. Table II).

Table IX suggests then that the higher the effort, the lower the catchability. ever, according to the theory used by most scientific workers in estimating nimal population sizes or the effect of exploitation, the catchability coefficient, ed by equation (8), is not dependent on the numbers of units of effort nded. On the basis of this study we question the applicability of the theory ndom search to the studies of lobster populations and other populations as when the density of the population is not very low and not exactly uniform.

ACKNOWLEDGMENTS

The source data for the analysis were given me by Dr D. G. Wilder who is arge of lobster studies at the Fisheries Research Board of Canada Biological on in St. Andrews. His views and intimate knowledge of the fishery have an integral part of the background necessary in developing this report.). W. McLeese has kindly provided me with the indices of activity.

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e Air Blowing of Cod Liver Oil. II. Changes in Fatty Acid mposition as Determined by Gas–Liquid Chromatography[1]

By P. M. Jangaard, R. G. Ackman, R. D. Burgher and M. L. Hughes

Fisheries Research Board of Canada
Technological Station, Halifax, N.S.

ABSTRACT

The effect of air blowing at two temperatures, 80 and 130°C, on the major component fatty ls of cod liver oil has been determined. As expected, the proportions of the highly unsaturated y acids drop rapidly, especially at the higher temperature investigated. The saturated acids virtually unchanged under the conditions employed, while the proportion of monounsaturated ls shows only a slight drop.

INTRODUCTION

MEROUS AUTHORS have studied the oxidation of fats, oils, and pure fatty terials under a variety of conditions. However, only through the develop-nt of gas–liquid chromatography in the last decade has it become possible to idly follow the effect of oxidation and polymerization on the individual fatty ds.

In an earlier report from this laboratory (Jangaard and Ackman, 1962), effect of air blowing on the physical and chemical constants of cod liver oil, l oil and herring oil was determined. Samples recently taken to study the anges occurring in the individual fatty acids during blowing at 130° have been verted to methyl esters and analyzed by gas–liquid chromatography. mples collected during two earlier experiments at 80 and 130° have also been estigated.

Greaves and Laker (1961) studied the heat bodying of linseed oil at 293° d found that only the polyunsaturated acids decreased appreciably in 6 hr. estone *et al.* (1961) heated cottonseed oil at 205° for 300 hr and reported that linoleic acid content dropped from 50 to 13% while the saturated and mo-unsaturated acids were unchanged. Endres *et al.* (1962) reported losses of th lauric and oleic acids while bubbling air through purified triglycerides at ° and suggested that these acids were broken down to short-chain fragments d removed along with the volatile products.

EXPERIMENTAL

The apparatus used for the air blowing is described in an earlier communica-n (Jangaard and Ackman, 1962). The samples investigated in the present dy were the previously reported No. 12 and 24, blown at 80 and 130° respec-ely, and a new run, No. 27, also at 130° but with a different rate of air blowing.

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[1] Received for publication September 6, 1962.

Fish. Res. Bd. Canada, 20(1), 1963.
nted in Canada.

The methyl esters used for gas–liquid chromatographic analyses were prepared by methanolysis employing sodium hydroxide as the catalyst. Samples of oil (5 g) from experiments 24 and 27 were refluxed with methanol (5 ml) and 0.5*N* methanolic NaOH (3 ml), cooled, petroleum ether (30–60°) was added and the reaction mixture transferred to a separatory funnel. The glycerol settled out and was discarded and the petroleum ether layer was then washed with water (4 times in 10 ml lots), followed by saturated sodium sulfate solution and dried. The petroleum ether was removed *in vacuo*.

In experiment No. 12, where some of the samples were more viscous and the free fatty acid content attained 4 to 5%, oil (5 g) was refluxed with methanol (5 ml) and 0.5*N* methanolic NaOH (5 ml). Some difficulty was experienced in dissolving the more highly polymerized material in petroleum ether. Methyl ethyl ketone was therefore employed and found satisfactory. The methyl ethyl ketone layer was washed and dried as before and the solvent removed *in vacuo*.

A Wilkens Aerograph model A-90 was used for the gas–liquid chromatographic analyses. The column was 10 ft in length of $\frac{1}{4}$-inch O.D. copper tubing, packed with DEGS polyester (20%) on GC-22 Super Support[2]. The oven temperature was 220°, and the carrier gas helium (inlet pressure 25 lb). Peak areas were determined by a Disc Instruments Inc. integrator fitted on a Minneapolis Honeywell Electronik 1 mv Recorder. Methyl laurate (about 5% w/w) was used as an internal standard in order to compensate for the various amounts of nonvolatile polymerized material in the samples, and the correction calculations carried out according to Mikkelsen and Richmond (1962).

RESULTS AND DISCUSSION

The gas–liquid chromatographic analyses are satisfactory with the exception of those samples with the lower proportions of eicosapentaenoic acid and docosahexaenoic acid. These have, at the sensitivity employed, a somewhat irregular baseline which may be partly due to artifacts such as conjugated acids of shorter chain length (e.g. octadecatetraenoate) which have increased retention times compared to the normal form (Morris *et al.*, 1960; Daniels and Richmond, 1960). Similarly, conjugated but unpolymerized forms of the longer chain polyenes cannot be accounted for by this procedure. It is, however, probable that these would be rapidly destroyed in the various reactions possible in the experiment and would not be present in a significant proportion. Since response factors (Horrocks, 1961) are not available for the polyunsaturated acid esters involved, it is assumed, for simplicity, that area percent is equivalent to weight percent.

In Table I, the "A" columns tabulate the weight percentages of eight of the major component fatty acids in cod liver oil from run No. 27. The apparent column "B" the results when calculated against a constant figure for palmitic acid (13.0).

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[2] The Coast Engineering Laboratory, Hermosa Beach, Calif.

Run No. 27, 130°C, air flow 6500 ml/min

	Sample No:	1		2		3		4		5		6		7		8	
Acid	Original cod liver oil (weight percent)	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
14:0	5.5	5.2	5.2	5.0	5.6	5.0	5.2	5.8	5.6	5.2	5.3	6.0	5.5	5.7	5.5	5.1	5.4
16:0	13.0	13.1	13.0	11.5	13.0	12.6	13.0	13.5	13.0	12.8	13.0	14.3	13.0	13.6	13.0	12.4	13.0
16:1	15.0	14.8	14.7	13.1	14.8	13.4	13.8	14.6	14.1	13.2	13.4	15.7	14.3	16.5	15.8	13.0	13.6
18:0	3.6	3.4	3.4	3.3	3.7	3.2	3.3	3.5	3.4	3.1	3.2	3.8	3.5	3.2	3.0	2.5	2.6
18:1	24.5	24.3	24.1	21.6	24.4	22.5	23.2	24.4	23.5	22.1	22.4	25.5	23.2	23.4	22.4	20.2	21.2
20:1	15.8	16.0	15.9	13.9	15.7	14.4	14.9	15.4	14.8	14.4	14.6	15.7	14.3	15.0	14.3	12.8	13.4
22:1	8.3	7.7	7.6	6.7	7.6	7.4	7.6	7.8	7.5	7.2	7.3	8.1	7.4	7.2	6.9	7.4	7.8
20:5	8.2	5.7	5.7	5.4	6.1	5.6	5.8	4.9	4.7	4.6	4.7	3.8	3.5	2.4	2.3	2.3	2.4
22:6	6.1	3.9	3.9	4.4	5.0	3.6	3.7	3.4	3.3	2.1	2.1	1.8	1.6	1.9	1.8	1.4	1.5
Totals:			93.5		95.9		90.5		89.9		86.0		86.3		85.0		80.9
Iodine value	168	154		–		141		–		127		–		115		110	
Viscosity stokes (25°)	0.5	0.6		–		1.3		–		2.25		–		5.0		6.2	
Blowing time (hr)	0	0.5		1		1.5		2		3		4		5		6	

increase in unreacted saturated acids as the polymerization proceeds has been avoided by the use of methyl laurate as an internal standard for the gas–liquid chromatographic analyses. However, the results still show some scattering, and they were therefore recalculated with a constant value (13%) for palmitic acid and tabulated in column "B". Esposito and Swann (1962) have shown that transesterification does not give consistent quantitative results with alkyd resins. Saponification and esterification of the isolated fatty acids with diazomethane might be helpful with certain viscous samples, although the erratic results are perhaps due to the polymers affecting the ester recovery procedure.

From these data it can be seen that the saturated acids are unchanged after air blowing at 130° for 6 hr, the amount of monounsaturated acids decreases slightly (1 to 3%) and the major highly unsaturated acids, eicosapentaenoic and docosahexaenoic acids, practically disappear.

The samples from two earlier runs, No. 12 blown at 80° and No. 24 blown at 130° were also esterified and analyzed (Table II). Some of the component fatty acids showed an increase in concentration in the first hour before levelling off, especially the palmitic, palmitoleic and oleic acids. Since this rise does not occur in samples from run No. 27 which were esterified and analyzed immediately,

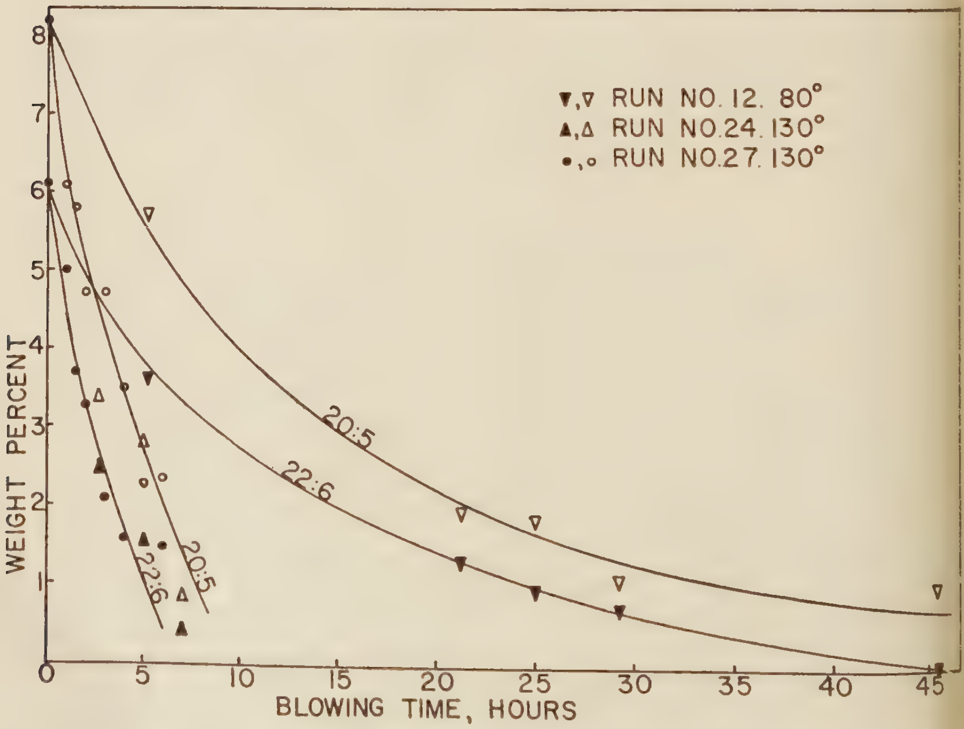

FIG. 1. Reduction in the percentage of eicosapentaenoic and docosahexaenoic acids in the air blowing of cod liver oil. The results are calculated with a constant value for palmitic acid (Column "B", Tables I and II).

column "B" the results when calculated against a constant figure for palmitic acid (16:0).

		Run No. 12, 80° air flow 6500 ml/min										Run No. 24, 130°, air flow 9500 ml/min					
	Sample No:	1		2		3		4		5		1		2		3	
Acid	Original cod liver oil (weight percent)	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
14:0	5.5	6.7	4.8	6.8	4.9	7.1	4.8	7.7	4.9	7.7	4.8	7.3	5.5	6.9	5.5	6.4	5.4
16:0	13.0	18.4	13.0	18.1	13.0	19.2	13.0	20.5	13.0	20.8	13.0	17.4	13.0	16.3	13.0	15.3	13.0
16:1	15.0	17.0	12.1	16.0	11.6	16.7	11.4	17.1	10.9	17.5	11.0	18.3	13.7	17.3	13.8	16.2	13.8
18:0	3.6	4.7	3.3	4.1	3.0	4.4	3.0	4.5	2.9	4.9	3.1	4.5	3.4	3.9	3.1	4.1	3.5
18:1	24.5	32.1	22.9	30.5	22.0	32.7	22.3	33.5	21.4	34.4	21.7	30.9	23.1	28.0	22.3	26.0	22.1
20:1	15.8	15.3	10.9	14.9	10.7	15.7	10.7	16.3	10.4	17.4	11.0	19.9	14.9	17.9	14.3	16.1	13.7
22:1	8.3	8.9	6.3	7.6	5.5	8.1	5.5	7.5	4.8	8.9	5.6	10.4	7.8	8.4	6.7	8.2	7.0
20:5	8.2	8.0	5.7	2.6	1.9	2.5	1.7	1.7	1.1	1.6	1.0	4.4	3.3	3.4	2.7	1.0	0.9
22:6	6.1	5.0	3.6	1.8	1.3	1.3	0.9	1.1	0.7	0	0	3.3	2.5	1.9	1.5	0.5	0.4
Totals:			82.6		73.9		73.3		70.1		71.2		87.2		82.9		79.8
Iodine value	168	150.1		116.3		113.3		109.5		98.8		120		105		98.5	
Viscosity stokes	0.5	0.85		7.2		10.7		24.4		63.4		3.3		9.6		22.7	
Blowing time (hr)	0	5¼		21¼		25		29¼		45½		2¾ hr		5		7	

it is probably due to the fact that the samples were stored for several months before esterification. However, by calculating the results relative to a constant value for palmitic acid (13%), these results can be compared with those from run No. 27. The results from runs No. 24 and 27, both blown at 130°, correlate well, showing that these assumptions are valid.

In Fig. 1 the effects of air blowing at the two temperatures (80° and 130°) on the eicosapentaenoic and docosahexaenoic acids are plotted. As is to be expected, the decrease in concentration of these acids is much more rapid at 130°, the docosahexaenoic acid content approaching zero in 43 hr at 80° and in 7 hr at 130°. The saturated and monounsaturated acids at 80° show very little change except for a rise in the first hours as previously mentioned, which becomes a slight drop when the results are calculated to a constant value for palmitic acid.

Greaves and Laker (1961) have pointed out that during heat polymerization of linseed oil the content of linoleic and linolenic acids drops from 71% to 16%, thus a total of 55% of the fatty acids have polymerized to produce a stand oil with a viscosity of 70 poises. By air blowing cod liver oil, an oil of similar viscosity can be obtained with the oxidative polymerization of two highly unsaturated fatty acids totalling approximately 15% of the original fatty acid composition. This would explain the superior performance of linseed oil in paints and varnishes as compared to polymerized marine oils since the bulk of the oil is made up of relatively inert fatty acids. Rapeseed oil is mainly used for the production of blown oils for lubrication. This oil contains about 25% polyunsaturated acids (Hilditch, 1956), and blown cod liver oil should therefore have properties similar to blown rapeseed oil.

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Resumption of Feeding by and Survival of Adult Sockeye Salmon *(Oncorhynchus nerka)* Following Advanced Gonad Development[1]

By J. R. McBride, U. H. M. Fagerlund, M. Smith and N. Tomlinson

Fisheries Research Board of Canada
Technological Station, Vancouver 8, B.C.

ABSTRACT

Adult, migrating, fasting sockeye salmon (*Oncorhynchus nerka*) were held in captivity in fresh water without spawning well beyond the time when they would normally have done so and died. A few of the fish were then gonadectomized and force feeding was begun. A few unoperated fish were fed similarly while the remainder served as unoperated, unfed controls. The gonads of the operated fish were well developed. After a period of feeding of about four months some fish in each group had survived. The fed fish had regained their green color and much of their weight and vigor, while the surviving unfed fish were extremely emaciated and listless. At this time voluntary feeding by the force-fed fish was observed for the first time, and it was then found that the five surviving unfed controls would also take food voluntarily. While two of these fish died without apparent improvement in their condition, the other three gradually regained green color, weight and vigor.

INTRODUCTION

Adult, anadromous pacific salmon (*Oncorhynchus*), alone amongst the Salmonidae, always die after their first reproductive cycle (Clemens and Wilby, 1961) and the association of death with sexual maturation has been extensively investigated both physiologically and histologically from the comparative point of view (Robertson *et al.*, 1961, and earlier papers; Schmidt and Idler, 1962). In the present communication we wish to describe some experiments with adult sockeye (*Oncorhynchus nerka*) which demonstrate that they can survive extensive gonad development.

METHODS AND MATERIALS

Sockeye Salmon

The fish were captured on their spawning migration from the North Pacific as they entered Great Central Lake, Vancouver Island, B.C. during July and September 1961. Normally these fish spawn from late September until the end of November on lakeshore beaches and in creeks feeding the lake. They die within a few weeks of spawning. Salmon collected in July developed secondary sexual characteristics (Clemens and Wilby, 1961) during August 1961. These characteristics were already present in fish captured in September 1961. Both groups contained males and females. The fresh water aquaria in which the

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[1] Received for publication August 7, 1962.

J. Fish. Res. Bd. Canada, **20**(1), 1963.
Printed in Canada.

fish were held and the treatment of fungal infections with 3% aqueous sodium chloride and 2-phenoxyethanol have been described (Idler *et al.*, 1961). Weekly intramuscular injections of Terramycin (0.5 ml of intramuscular solution, 50 mg/ml, Pfizer Canada, Montreal 9, Quebec) were employed to control a bacterial infection tentatively identified as furunculosis (personal communication, B. A. Southcott). Treatments were continued for six to ten weeks and were effective in removing the external symptoms of disease in infected fish and also in preventing the appearance of disease in healthy fish kept in the same aquaria. Water temperatures ranged from 12°C in August 1961 to a low of 4°C in December 1961 to February 1962, followed by an increase to 12°C in July 1962. Aquaria were covered with fibreglass sheets to contain the more exuberant fish. The light intensity immediately below these covers (5 cm above the water surface) ranged from 20–50 lux and was maintained constant at all times. The aquaria did not contain gravel.

Bilateral Gonadectomy

The procedure of Robertson (1958) was employed except that plain 000 sterile surgical gut was used to close the abdominal incision. Stitches were removed after ten weeks. Fig. 1 shows an operated female fish in operating position. The ovaries are in the beaker to the right of the fish and illustrate the degree of development of these organs at the time.

Force-feeding Technique

Forced feeding of the fish was carried out by means of a 10-ml syringe, the tip of which had been expanded and fitted with a 15-cm length of 3-mm inside diameter polyethylene tubing. Food prepared in the form of an aqueous slurry (see below), was drawn into the syringe, the tube was gently inserted into the fish's stomach via the esophagus and the food was then expelled from the syringe into the stomach. In order to minimize the possibility of injuring the fish during the force-feeding procedure they were anaesthetized in a 1 in 4500 parts solution of 2-phenoxyethanol. The period of forced feeding was divided into three phases. Phase I included the first two weeks during which time each fish was given 3 ml of a 60% aqueous sustagen (Mead Johnson of Canada Ltd., Toronto, Ontario) slurry on three alternating days each week. As a supplement to this diet, each fish was given a 0.2-ml intramuscular injection of vitamins ("Amvitol", Walker Vitamin Products, Inc., Mount Vernon, New York) on the last feeding day of each week. Phase II extended from the third week of feeding to the end of the sixth week. During this period the dosage of 60% sustagen was increased from 3 to 7 ml. The prepared diet of Phase III, which extended from the end of Phase II to the termination of forced feeding, contained a higher percentage of solids than those for Phases I and II. It consisted of 40% canned salmon, 20% beef liver, 20% beef heart, 10% zooplankton, 5% Pablum and 5% water. The meat was finely ground and then mixed with the Pablum and water to form a suspension. Each fish was given 7 ml of this preparation on Tuesday and Thursday of each week.

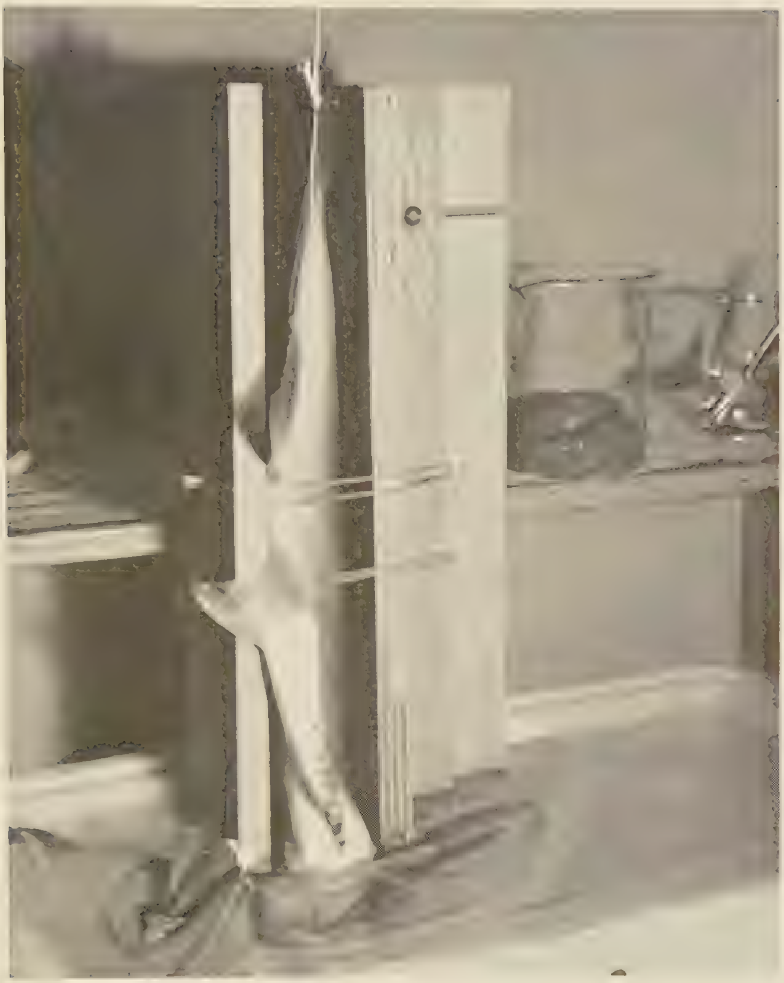

FIG. 1. Operated female sockeye. Ovaries in beaker to the right of the fish.

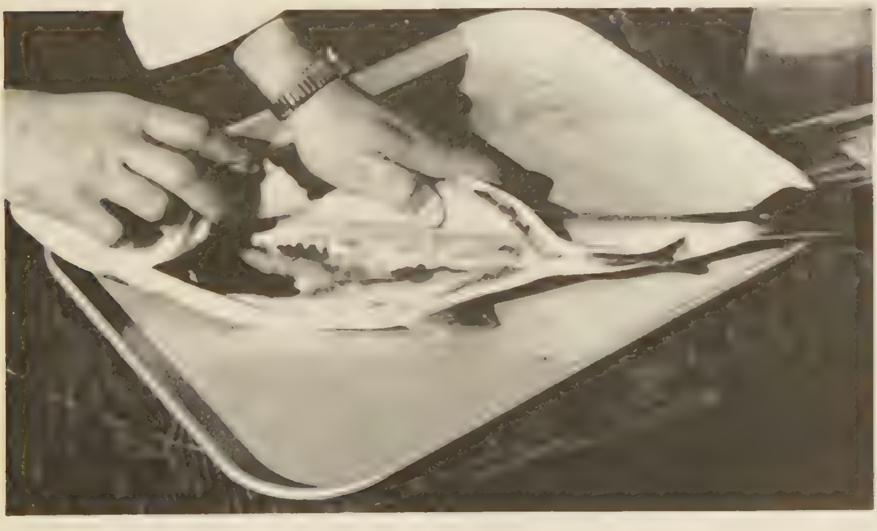

FIG. 2. Ovaries of sockeye about 4 months beyond expected spawning time. Posterior portion of ovaries has been removed to show degeneration of ova at anterior section. A few normal appearing ova can be seen in the visceral cavity.

RESULTS

Of the 59 salmon captured in July 1961, and the 16 captured in September 1961, 26 and 9 fish respectively were alive in mid-December 1961. At this time there were no detectable differences in the external secondary sexual characteristics of the two groups. All the males had elongated hooked jaws, many also had teeth. These fish did not have the red body coloration often seen in male *O. nerka* during the spawning run. In general for fish of both sexes, scales had been absorbed. A few females retained their silver green coloration. However, the majority displayed the typical spawning coloration of females and all had distended, soft visceral regions indicating ovaries in an advanced stage of development. Both males and females, having been kept three or five months without feeding, were emaciated.

Between mid-December 1961 and mid-January 1962, the fish were divided into three groups: (i) two males and three females which were force-fed as described above (mid-December 1961); (ii) one male and six females which were gonadectomized (mid-January 1962). After 48 hours (two fish died in this period) force-feeding was started as above; (iii) 14 males and 9 females were kept unfed as in the previous 3–5 months. In group (ii) the gonads of the male weighed 30 g, while the gonads of the females varied in weight from 143 to 218 g. The diameter of the ova ranged from 4.00 to 5.5 mm. These weights contrast with average weights of 15 g (for 5 males) and 78 g (for 14 females), respectively, for fish taken in July. Force-feeding was continued until early in May 1962, at which time one male and one female in each of groups (i) and (ii) (force-fed fish) remained alive together with 5 males in group (iii).

Of the 8 fish which died in groups (i) and (ii), 7 had pink flesh whilst the eighth fish had grey flesh streaked with pink. All 8 fish had visible scales (overall silvery appearance). Of the 18 unfed fish which died in group (iii), 14 had grey flesh and 4 had grey flesh streaked with pink Only 4 fish in this group had visible scales and these were distributed in irregular patches along the sides, back and abdomen. Gonad degeneration was evident in many of the dead fish from groups (i) and (iii). Fig. 2 shows the gonads of a typical female. The anterior portions consisted of a yellow pulp containing what appeared to be degenerating ova. The remainder of the gonads appeared normal, with eggs of 4.5 to 5.0 mm diameter. Several fish, both fed and unfed, developed a distinct yellow coloration a few weeks prior to death (Fig. 3). Both males and females exhibited this phenomenon and on *post-mortem* examination the livers of the fish so affected were found to be jade green in colour rather than the usual dark brown.[2]

During the first week of May 1962, the external features of the fish remaining alive were carefully examined. The 4 fed fish (groups (i) and (ii) had abundant visible scales distributed over their sides, back and abdomen. Microscopic examination of these scales showed that they were partially degenerated and no new growth was evident (S. R. Killick, personal communication). The sides of the fish were silvery and the back green. However, the males retained their elongated hooked jaws and teeth. Only one of the 5 unfed fish (group (iii)) had visible scales and these were sparsely and irregularly distributed. The skin of the unfed fish was a dull brown colour (Fig. 4). From March 1962, semi-frozen pellets of the wet diet were periodically placed in the aquaria containing the force-fed salmon. However, it was not until early May 1962, that the fish were seen to eat the pellets. The intake of pellets by the fish increased during May and force-feeding was discontinued at the end of the month. By July 1962, the fish were feeding avidly twice daily and increasing in weight by about one tenth of their body weight per month. At the beginning of May 1962, an attempt to feed the five remaining salmon in group (iii) was made. These fish were very thin, three of them had developed twisted backs (Fig. 5) and all were sluggish in their movements. However, they ate pellets at the first attempted feeding, albeit in a very dilatory manner, and during the first three weeks of feeding two fish died without change in external appearance or increase in weight. Subsequently the remaining fish fed more actively, and behaved much more vigorously. During June–July 1962, they increased in weight at the same rate as fish in groups (i) and (ii).

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[2] We have entertained the possibility of jaundice as the underlying cause of the yellow coloration of the skin and the green appearance of the liver. The final diagnosis, however, will rest upon a biochemical and histological study of the tissues involved, but as a matter of interest, it may be reported that these symptoms are some of the characteristics of jaundice in humans (Harrison *et al.*, 1958).

DISCUSSION

To the best of our knowledge the present report constitutes the first demonstration of the resumption of feeding by and subsequent survival of adult anadromous sockeye salmon after a period of fasting during which they would normally have spawned and died, and demonstrates that the "ripening"[3] process leading to spawning does not inevitably result in death within a relatively limited period of time. Factors that probably contributed to the success of the present study include effective control of fungal and bacterial infections to which *O. nerka* is very susceptible in fresh water, and the use of aquaria (Idler *et al.*, 1961) which minimize physical damage. Water temperature could also be a significant factor (Phillips and Livingston, 1960). Although force-feeding hastened the recovery of the fish it is evident that it is not a prerequisite for resumption of feeding by *O. nerka*.

The physical changes in the fed fish are of some interest. Associated with the feeding there was a return to silver green coloration, and this change was coupled with an increased coloration of the muscle, greatly increased vigor and marked increase in weight. However, there was no loss of other secondary sexual characteristics such as the elongated hooked jaws and teeth. This suggests that the reversible changes may be more directly connected with starvation than with sexual changes. Related phenomena have been observed (White, 1942) in post-spawned Atlantic salmon (*Salmo salar*). The non-spawning of the salmon

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[3] We have used the term "ripening" to describe that process within the gonads through which the eggs and sperm develop and are eventually released.

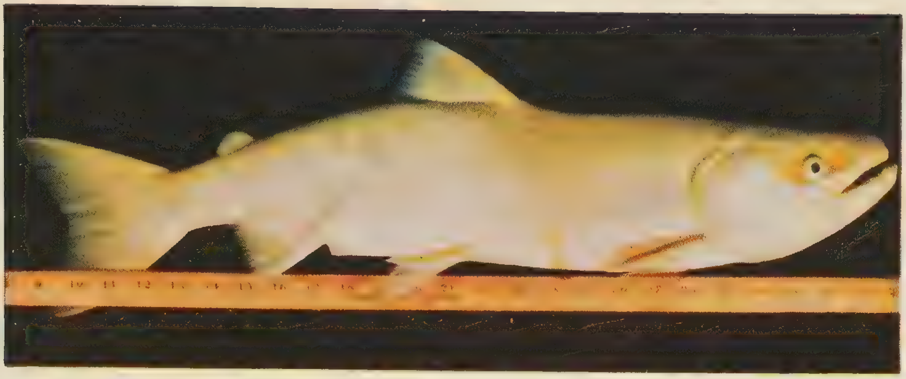

FIG. 3. Male sockeye showing external yellow coloration noted in many of these fish shortly before death.

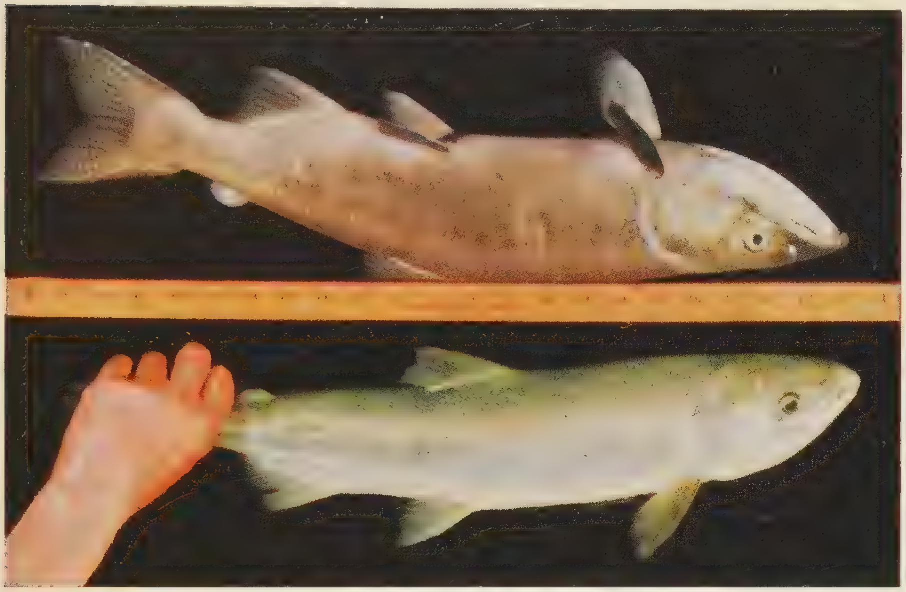

FIG. 4. Force-fed castrated male (top), unfed and unoperated male control (bottom), 4 months beyond normal spawning time. The operated fish has regained its green coloration during 4 months of feeding but has retained its elongated snout.

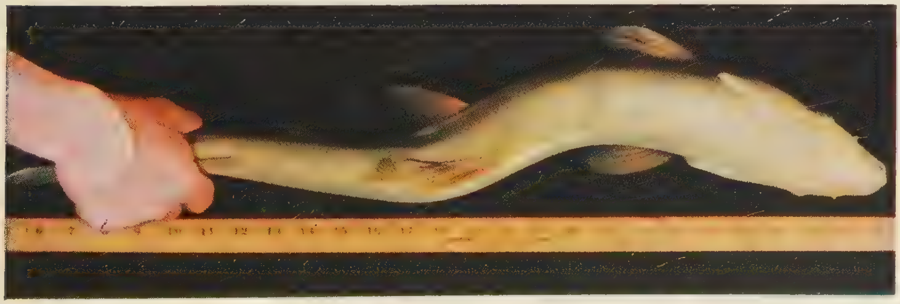

FIG. 5. Dorsal view of male sockeye showing emaciated condition following 9 months of complete starvation.

used in the present experiment raises a question as to the state of "ripeness" attained by the gonads of these fish. Certainly the state and weight of those from the gonadectomized fish indicate "ripening" was well advanced (Idler and Clemens, 1959). Environmental factors probably contributing to their failure to spawn would include the absence of gravel from aquaria (C. Groot, personal communication) and the lighting conditions (Burrows, 1958). The fact that gonadectomized fish survived as well as non-operated ones would encourage the hope that spawned adult fish can be induced to survive. Further encouragement is provided by the results of earlier investigations with precocious king salmon (*O. tshawytscha* Juv.) and with kokanee (*O. nerka* that spend their entire life in fresh water). Robertson (1957) demonstrated that many precocious male parr king salmon continued to live and grow at the normal rate after being artificially spawned. Furthermore, these fish exhibited a renewal of spermatogenesis five months after being stripped of their milt. Gebhards (1960) in a later study with the same fish confirmed Robertson's earlier findings. In the latter study it was noted, however, that 25% of the males were feeding at the time of spawning. Unlike adult salmon, these fish did not develop secondary sexual characteristics.

Doak (reported by Fraser, 1918) found that kokanee reared from the fertilized ova of sea-going sockeye not only matured during their third (male) or fourth (male and female) year but also a few survived following either artificial or natural spawning. The survivors which, like their progenitor, ceased to feed prior to spawning, were seen to take food actively and appeared perfectly mended two months after spawning. Their skin was bright silver in colour and scales were shed readily. Scales from these post-spawned fish, however, showed no indication of a spawning mark. The possibility that adult anadromous sockeye can survive spawning is under active investigation.

ACKNOWLEDGMENTS

The authors wish to thank Dr J. R. Brett, of the Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C., Messrs R. MacLaren and F. Boyd of the Department of Fisheries of Canada for the fish used in this investigation, Dr B. McK. Bary, Department of Zoology, University of British Columbia, for kindly supplying zooplankton, Dr W. S. Hoar, Department of Zoology, University of British Columbia, for his encouragement and helpful suggestions, and Mr S. R. Killick, International Pacific Salmon Fisheries Commission, for his examination and interpretation of scales taken from fish used in this study.

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Species Differences of Some Members of Salmonidae Based on Their Muscle Myogen Patterns[1]

By H. Tsuyuki and E. Roberts

Fisheries Research Board of Canada
Technological Station, Vancouver 8, B.C.

ABSTRACT

The muscle myogen patterns obtained by starch gel electrophoresis of the Dolly Varden and eastern brook trout (*Salvelinus*), the rainbow and steelhead trouts and the Atlantic salmon (*Salmo*), and the coho, spring, chum, sockeye and pink salmon (*Oncorhynchus*) are compared. The myogen protein patterns are clearly distinct for each species of fishes studied, except for the rainbow and steelhead trouts, and constitute a remarkably constant property which can be employed to differentiate between species and for other useful purposes. The specific and generic inter-relationships have been analyzed by these patterns and developed as further criteria for classification purposes and are discussed in conjunction with currently accepted beliefs.

INTRODUCTION

Differences in the muscle myogen protein components between various species of fishes have been studied by several methods. For example, by moving boundary techniques Connell (1953) found considerable differences in the myogen proteins of 18 species of fishes and more recently Lillevik and Schloemer (1961) in 10 species of the fresh water sunfish family. Nikkilä and Linko (1955) have shown differences in fishes by paper electrophoretic means. Column chromatography has also been used to some extent (Tsuyuki and Roberts, 1961; Tsuyuki *et al.*, 1962a). However, the highly sensitive starch-gel electrophoretic method first developed by Smithies (1955) and applied to the separation of myogen proteins of a variety of fishes by Thompson (1960), and to certain members of the Salmonidae family by Tsuyuki *et al.* (1962b), gave the most definitive results. The chief advantages of this method lie in its extreme sensitivity, the ease of manipulation, and its capacity to compare large numbers of samples simultaneously.

The present communication describes an extension of these studies and involves a direct comparison of the muscle myogens of *Oncorhynchus* (spring, sockeye and coho salmons) with *Salmo* (rainbow and steelhead trouts and Atlantic salmon). Two members of *Salvelinus*, Dolly Varden (*S. malma*) and eastern brook trout (*S. fontinalis*) are also compared. The results of these studies are discussed in relation to present knowledge of the taxonomic classification of the Salmonidae family.

MATERIALS AND METHODS

The preparation of the myogen extracts and the conditions for starch gel electrophoresis were precisely as described previously (Tsuyuki *et al.*, 1962a, 1962b). The starch gel was prepared in $0.023M$ sodium borate buffer at a pH of 8.5.

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[1] Received for publication July 17, 1962.

J. Fish. Res. Bd. Canada, **20**(1), 1963.
Printed in Canada.

The sockeye, spring, and coho salmon were obtained as described before (Tsuyuki *et al.*, 1962a, 1962b). The sample of Atlantic salmon was shipped frozen in dry ice by Dr D. R. Idler, Director, Fisheries Research Board of Canada Technological Station, Halifax, N.S. *Salvelinus fontinalis* was obtained live from the Cache Creek area in B.C., through the kind co-operation of Mr J. W. Cartwright, Regional Fisheries Biologist, Department of Recreation and Conservation, Williams Lake, B.C. The sample of *Salvelinus malma* was obtained frozen in dry ice from Cultus Lake, B.C.

RESULTS AND DISCUSSION

Certain basic differences are evident in the myogen patterns of sockeye salmon on the one hand and coho and spring salmon on the other (Fig. 1). Details of the differences within the genus *Oncorhynchus* have been described elsewhere (Tsuyuki *et al.*, 1962b). No apparent difference could be observed between the rainbow and steelhead trouts, while the Atlantic salmon shows the absence of a strong anionic zone at 2.5 cm, and the presence of weak anionic and cationic zones at 2.7 and 1.5 cm respectively from the origin (Fig. 1). Quantitatively, the major portion of the proteins in the rainbow and steelhead trouts are anionic at this pH while in the Atlantic salmon the distribution is more equally on either side of the origin and compares with the coho and spring salmon in this respect. Overall similarities are particularly evident between the genus *Salmo* and the coho salmon of the genus *Oncorhynchus*, indicating that these are closely related. Without further refinement in the method of protein separation, racial differences between the muscle myogens of sockeye salmon captured at Port Renfrew and Cultus Lake, B.C., could not be shown too clearly.

The muscle myogens of two species of *Salvelinus* are compared to that of rainbow trout in Fig. 2. The eastern brook trout lacks the most cationic component observed in the rainbow trout. Some minor differences are also evident in the most anionic components. The Dolly Varden is identical to the rainbow trout on the cathode side but possesses two additional anionic components at 0.8 and 1.5 cm from the origin. These two zones are absent in both the rainbow and eastern brook trouts. However, the 0.8 cm zone is present in the coho, spring and chum salmon (Fig. 1; Table I, protein zone j) while the 1.5 cm zone is present in the sockeye and the pink salmon (Fig. 1; Table I, protein zone k).

A summary of the myogen patterns of 3 species of *Salmo*, 2 of *Salvelinus*, and 5 of *Oncorhynchus* obtained in this and previous studies (Tsuyuki *et al.*, 1962b) is presented in Table I. The fishes are arbitrarily arranged in an order of increasing differences in relation to the number and position of protein zones compared to the rainbow and steelhead trouts. In general, the order appears to correspond with the view that *Oncorhynchus* has evolved from the *Salmo* (Milne, 1948; Neave, 1958; Regan, 1920; and Clemens, 1953) which in turn might be said to have arisen from *Salvelinus* (Dr C. C. Lindsey, personal communication). No attempt is made here to place the *Salvelinus* members in any category in relation to the other two genera. Since protein synthesis in the living organism occurs as a result of biosynthetic mechanisms controlled by

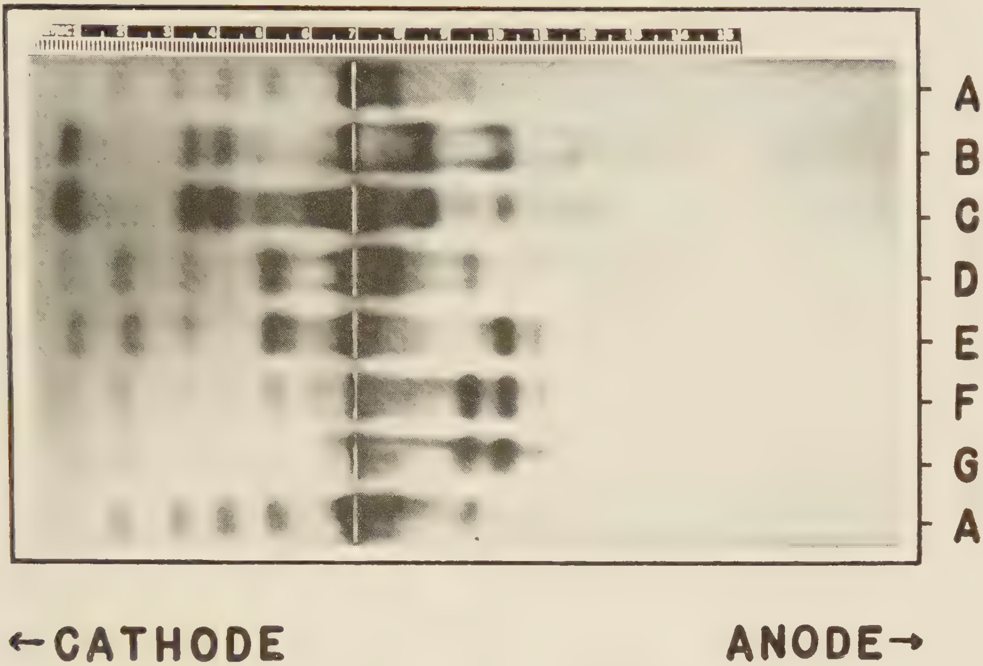
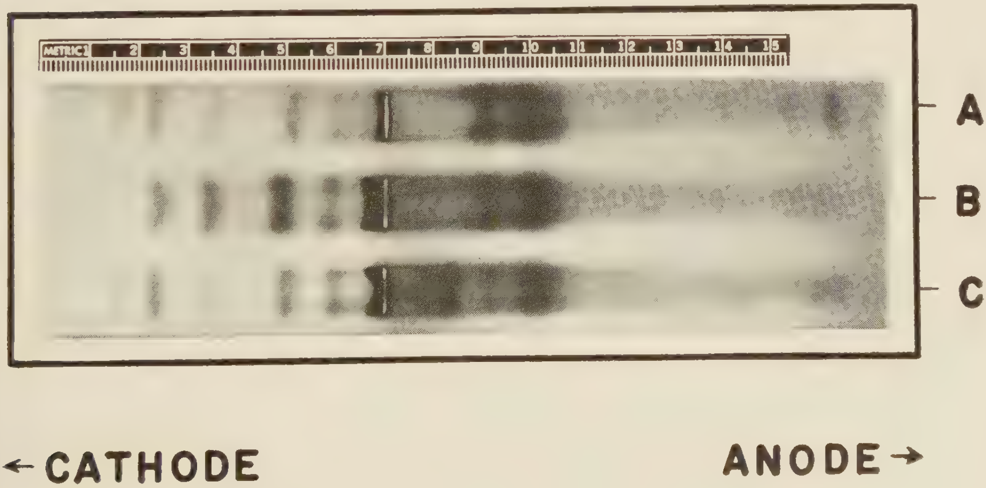

A
B
C
D
E
F
G
A
←CATHODE
ANODE→

FIG. 1. A comparison of the muscle myogen proteins of spring (A), Cultus Lake sockeye (B), Port Renfrew sockeye (C), coho salmon (D), Atlantic salmon (E), steelhead (F) and rainbow (G) trouts by starch gel electrophoresis.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ANODE→

FIG. 2. A comparison of the muscle myogen proteins of rainbow trout (A), eastern brook trout (B), and Dolly Varden (C) by starch gel electrophoresis.

TABLE I. Summary of the myogen protein patterns of 2 species of *Salvelinus*, 3 of *Salmo* and 5 of *Oncorhynchus*. These data have been compiled from this and other (Tsuyuki *et al.*, 1962b) communications. Letters a to p inclusive represent the positions where protein zones were found in the fishes though not necessarily all in any one species. A negative (–) sign indicates the absence and a positive (+) sign the presence of protein zones in the positions indicated by letters. Neither the relative intensities of the zones nor their mobilities are considered in this representation.

Species of fish	Maximum number of protein zones from the cathode to the anode																No. of zones differing from steelhead and rainbow trouts
	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	
Dolly Varden	–	+	+	+	–	+	–	+	+	+	+	+	–	+	+	–	2
Eastern Brook	–	–	+	+	+	+	–	+	+	–	–	+	–	+	+	–	2
Rainbow	–	+	+	+	–	+	–	+	+	–	–	+	–	+	+	–	
Steelhead	–	+	+	+	–	+	–	+	+	–	–	+	–	+	+	–	
Atlantic Salmon	–	+	+	+	–	+	+	+	–	–	–	–	+	+	+	–	4
Coho Salmon	–	+	+	+	–	+	–	–	–	+	–	+	–	–	+	–	4
Spring Salmon	–	+	+	+	+	+	–	–	–	+	–	+	–	–	+	–	5
Chum Salmon	–	+	–	+	+	+	+	–	–	+	–	+	–	+	–	+	8
Sockeye Salmon	–	+	–	+	+	+	+	–	–	–	+	–	–	+	–	+	9
Pink Salmon	+	+	–	+	+	+	+	–	–	–	+	–	–	+	–	+	10

fundamental genetic processes leading to differentiation, the product(s) of such reactions could be considered a measure of genetic differences and can be employed as another criterion for classification purposes. Each species of fish muscle myogen pattern examined so far is distinctly different and appears to be as characteristic as "fingerprints" for identification purposes. In this respect, the method will be extremely useful for identification of unknown samples of fresh frozen fish flesh, when other means are difficult to apply. In only one instance, namely, the rainbow and steelhead trouts, which are thought to be of one species (Clemens and Wilby, 1961; Carl, Clemens and Lindsey, 1959), was an identical pattern obtained. A remarkable degree of consistency of these patterns was observed between various adult individuals of any one species regardless of the sex or physiological condition (Tsuyuki *et al.*, 1962b).

In the genus *Oncorhynchus*, the two pairs comprised of the coho and spring salmon, and the sockeye and pink salmon differ from each other by only one zone position, while the chum salmon distinctly appear to lie somewhere between the two pairs though closer to the latter (Tsuyuki *et al.*, 1962b). In general, the coho salmon is closer to the rainbow trout than the spring salmon. Except for the close similarity of the coho and spring salmon the grouping of the remaining species of *Oncorhynchus* based on their myogen patterns deviates from that based on morphological, physiological, life-history, and behaviour studies by which the pink and the chum are found to be closely related and the sockeye salmon occupying a position intermediate between the two pairs (Clemens, 1953). Serological relationships (Hourston, 1949) indicated a close similarity among coho, spring and sockeye while the chum showed a significant difference. A preliminary comparison of the serum proteins (Tsuyuki and Gadd, 1962) of spring salmon, rainbow trout and the eastern brook trout indicate differences that are much less marked than their myogen patterns. New lines of preliminary evidence involving a general study of the multiple hemoglobins (Tsuyuki and

Gadd, 1962) of the spring and sockeye salmon in relation to the rainbow and eastern brook trouts definitely show a marked difference between the two species of *Oncorhynchus*, and further substantiates the relationships of the species of this genus arrived at by their myogen studies. The hemoglobin pattern of the spring salmon is remarkably close but not identical to those of the rainbow and eastern brook trouts.

Of the species of *Salmo* studied, the myogen patterns of the steelhead and rainbow trouts are identical as expected, while the Atlantic salmon differs somewhat. However, all the three species of *Salmo* show remarkable similarity to the coho salmon, followed closely by the spring salmon and distantly by the chum, sockeye and pink salmon, in this order. Although the cherry salmon (*O. masou*) has not been available for study, it would not be surprising if its myogen pattern was even closer to *Salmo* than to the coho salmon. One cationic zone at a position 3 cm from the origin (Fig. 1) progressively increased in intensity from an extremely faint band in the Atlantic salmon on through the coho and the spring to a strong zone in the sockeye salmon. The original stained starch gel patterns showed this gradual transition more clearly.

Both the Dolly Varden and the eastern brook trout (*Salvelins*) rare quite similar to the rainbow trout. It is interesting to note that one but not both of the two protein components (Table I, protein zones j and k) present in Dolly Varden and absent in the eastern brook, rainbow, steelhead trouts, is present in every member of *Oncorhynchus*.

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1962b. *Ibid.*, **40**: 929–936.

Comparative Ecology of Two Sympatric Species of Dace *(Rhinichthys)* in the Fraser River System, British Columbia[1]

BY J. H. GEE[2] AND T. G. NORTHCOTE

Institute of Fisheries, University of British Columbia
Vancouver, B.C.

ABSTRACT

Age, growth and food habits of leopard dace (*Rhinichthys falcatus*) in the lower Fraser River are described. Although recently emerged leopard dace and longnose dace (*Rhinichthys cataractae*) occur together in regions of slow or no current along the river margin, older longnose dace soon begin to occupy regions of higher water velocity. Yearling and older leopard dace remain predominantly in areas of little current. Laboratory experiments in a stream tank demonstrate a strong current preference in longnose dace fry, yearlings and adults. Leopard dace of comparable size show no preference for water current. The swimbladder volume of yearling and adult longnose dace is much lower than that of leopard dace, possibly an adaptation of the former species to occupation of riffle habitat. Temporary coexistence of the two closely related species in the same niche is discussed briefly.

INTRODUCTION

THE LEOPARD DACE, *Rhinichthys falcatus* (Eigenmann and Eigenmann), is a small cyprinid fish confined in its distribution to the Fraser and Columbia River systems. Although it is a common fish in both rivers, little is known about its life history. A closely related species, the longnose dace, *R. cataractae* (Valenciennes), also occurs in both river systems and has been collected in British Columbia from the same areas as leopard dace in the lower Fraser River. The sympatric occurrence of two congeneric species suggests a possible competitive relationship, opposing Gause's contention (Gause, 1934). The present study describes some life history features of leopard dace and examines the comparative ecology of both species in an attempt to explain their coexistence.

Published material on the life history of leopard dace is scant. Eigenmann and Eigenmann first described the species in 1893. Gilbert and Everman (1895) gave a morphological description with emphasis on nuptial tubercles. A brief, comparative food study of longnose and leopard dace was completed by Johannes (1958).

The term "habitat" will be used in reference to the physical environment of the fish, while "ecological niche" will designate the place of the fish within its biological environment. These definitions follow closely those of Elton (1927) and Grinnell (1928), as recommended by Udvardy (1959).

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[1] Received for publication June 29, 1962.

[2] Present address: Fisheries Research Board of Canada, Biological Station, St. Andrews, N.B.

J. FISH. RES. BD. CANADA, **20**(1), 1963.
Printed in Canada.

MATERIALS AND METHODS

Collection of Field Data

Leopard and longnose dace were collected by seines (2 mm diameter nylon mesh) from two areas in the Fraser River drainage system. The majority of collections were made in the lower Fraser River between Hope and Chilliwack; some were taken at MacAllister, further upstream.

Seine hauls were made in a wide variety of habitats but each haul was completed, when possible, in an area relatively constant in water velocity and depth over a 10 m length of homogeneous bottom. Thus fish collected in each haul were taken from a fairly specific type of habitat.

Stomach Content Analysis

Fish collected between Hope and Chilliwack were utilized for analysis of stomach contents. Contents of the anterior one third of the alimentary canal were emptied into a watch glass and identified. Food components were classified to genus where possible, and for each stomach, the number of organisms in each food group was recorded. The percent volume that each food group contributed to the total individual stomach volume was estimated.

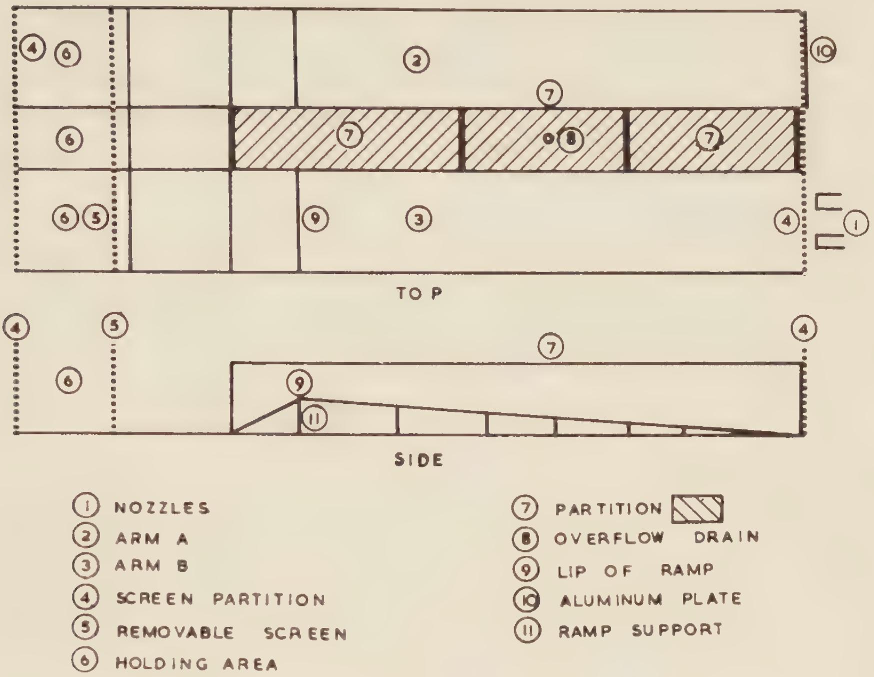
After identification, stomach contents of each fish were dried, placed in a calibrated glass tube, and the displacement volume recorded.

Laboratory Experiments

Laboratory experiments were conducted in a circular stream tank, described by Northcote (1962). One section of the stream tank was modified into an experimental section where all experiments were confined. The basic design was to provide two areas, one with current and one without current, for selection by experimental fish. Selection of a current area was taken to be an indication of current preference.

Two nozzles, connected to water pumps by flexible plastic pipes, could direct water currents into arm A or arm B of the experimental section (Fig. 1). Two screens at each end of the experimental section separated it from the remainder of the stream tank, while a third removable screen formed an area where fish were held prior to each experiment. An aluminum plate was placed against the screen at the head of the non-current arm to minimize any currents created by water circulating in the stream tank. The partition separating the two arms housed an overflow drain which removed excess water added in the non-experimental section to minimize fluctuations in water temperature. Water temperature in the stream tank remained between 6.5 and 8.5°C during all experiments.

The bottom of each arm sloped upwards towards the downstream end, terminating at the lip of the ramp in a downward slope (Fig. 1, side view). The upward slope was required to create a more uniform water velocity along the length of the current arm. Immediately below the current arms the tank bottom was marked off into six squares to give additional records on current distribution of experimental fish.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SIDE
① NOZZLES
② ARM A
③ ARM B
④ SCREEN PARTITION
⑤ REMOVABLE SCREEN
⑥ HOLDING AREA
⑦ PARTITION ▨
⑧ OVERFLOW DRAIN
⑨ LIP OF RAMP
⑩ ALUMINUM PLATE
⑪ RAMP SUPPORT

FIG. 1. Experimental section of stream tank.

Experimental fish were collected from three locations in British Columbia: the Nicola River at Merritt, Brunette Creek at New Westminster and the Fraser River at Chilliwack. These fish were held in a single hatchery trough in which there was virtually no current, although a slight turbulence occurred at one end where water was introduced. Water temperatures in the hatchery trough varied between 5 and 6.5°C during the experimental period.

Experimental fish were separated into three size groups: 30–40 mm, 50–70 mm and 71–95 mm, fork length. Three current preference tests were completed on the two larger size groups at each of four water velocities: 0.3, 0.6, 0.9 and 1.2 m/sec (1, 2, 3 and 4 ft/sec). Three experiments at velocities of 0.3 and 0.6 m/sec were made on 30–40 mm fish. Of the group of three experiments on a size group at each flow, two were made with the current in one arm while the third was completed with the current in the opposite arm. Water current was measured on the lip of the ramp with a Gurly flow meter. In all preference tests five pairs of fish were used; each pair was composed of approximately equal size specimens of the two species.

Prior to each experiment the appropriate velocity was created in the selected current arm. Water current was regulated to minimize surface bubbles and to equalize, as much as possible, flow along the length and width of the current arm. After the required velocity was established, the removable screen was placed in position.

Fish were then placed into the holding area of the experimental section and held there for a 30-minute period after which the removable screen was lifted out allowing fish to swim into any area. Observations on the current distribution of the ten experimental fish were made at 30-minute intervals for a 10-hour period following the removal of the screen.

Volume Analysis of Swimbladders

Swimbladder volume was measured on 75 leopard dace and 97 longnose dace taken in the Fraser River drainage below MacAllister. In volume determinations, the swimbladder was removed from the fish and its volume measured by inflating the collapsed airbladder in a water-filled tubular glass apparatus (calibrated to .01 ml).

LIFE HISTORY OF LEOPARD DACE

Age and Growth

The length–frequency method was used to distinguish age groups of leopard dace (Fig. 2). Young-of-the-year were collected in the lower Fraser River during August 16–18, 1960 while age group I and older were taken there on June 2 and 5, 1961. Sex was determined on all fish larger than 40 mm. As no obvious differences in length distribution were found between sexes, length frequencies of both sexes were combined.

Three distinct age groups — 0, I and II, — are evident in Fig. 2. Probably most fish between 60 and 80 mm in length are age III while larger individuals are age IV or older.

Growth in length and weight is illustrated for both sexes in Fig. 3. Fish of age I and older were taken from the June 2 and 5 collections (1961) while fish of age 0 were collected during August 16–18, 1960. Female fish are heavier and slightly longer than male fish; such differences in weight become more evident among older fish.

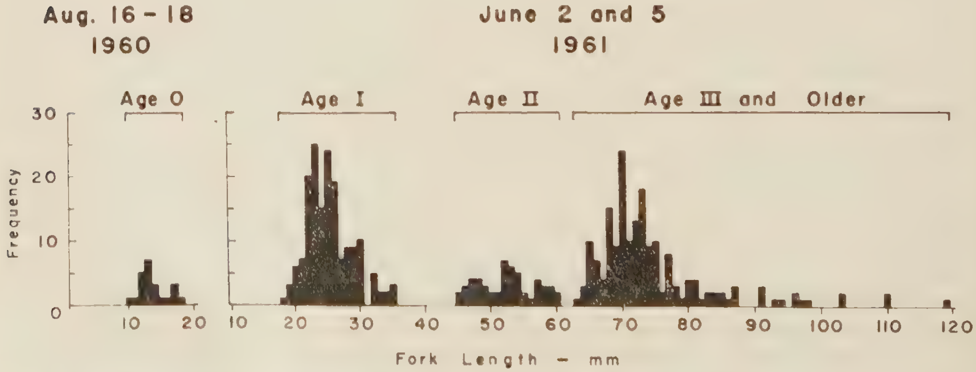

FIG. 2. Length frequency distribution of 420 leopard dace collected during summer (1960, 1961) in the lower Fraser River.

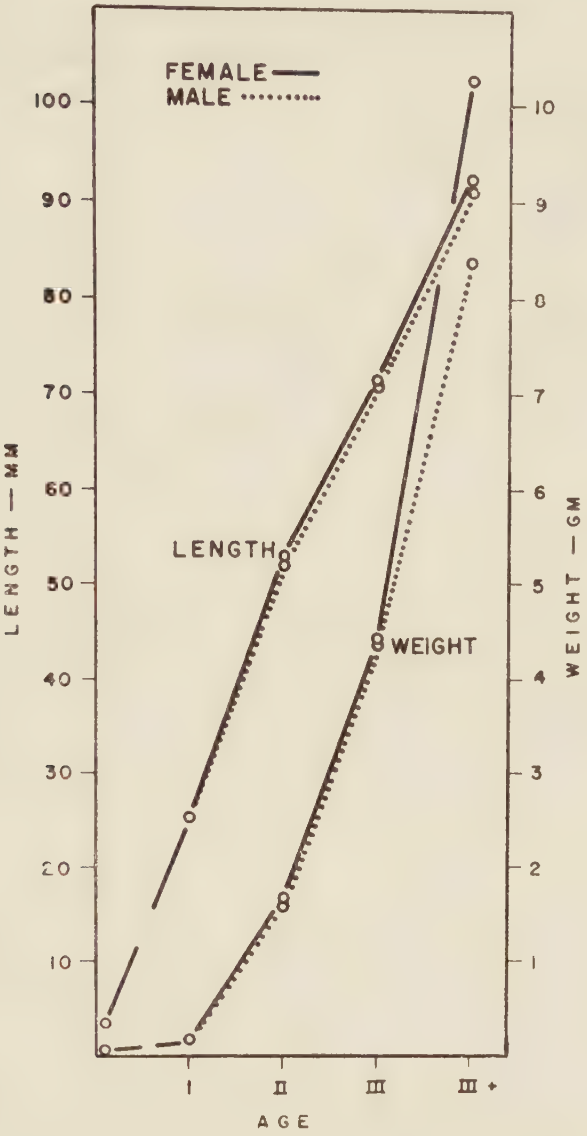

FIG. 3. Growth in length and weight of leopard dace from lower Fraser River. (Age III fish include all those between 61 and 80 mm fork length; III + all between 81 and 120 mm.)

FOOD HABITS

During high water level of the Fraser River in June and July, yearling leopard dace fed primarily (by volume) on aquatic insect larvae (Fig. 4). Ephemeroptera and Diptera were the most predominant forms. Adults (age II and older) fed primarily on *Lumbricus* and aquatic insect larvae, with Ephemeroptera and Diptera again dominant forms. *Lumbricus* becomes most available in high water due to its displacement from the substrate (Campbell, 1957).

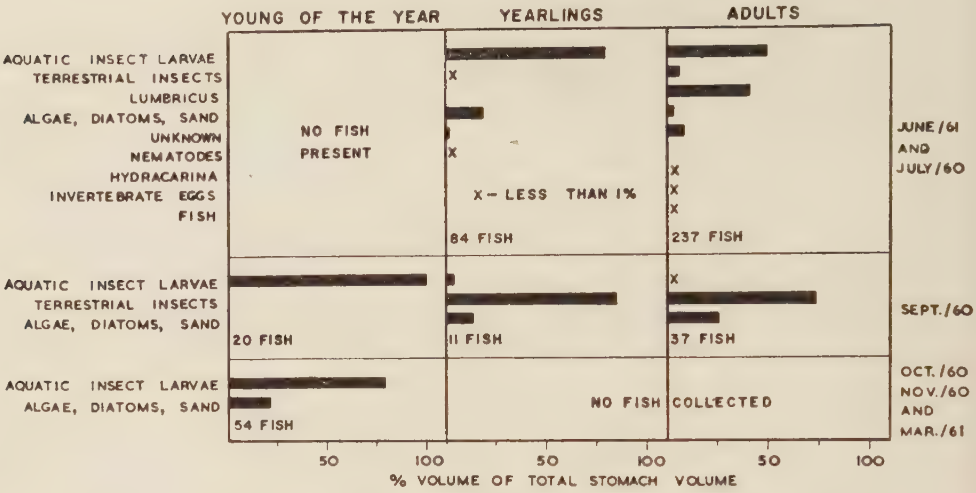

FIG. 4. Stomach contents of leopard dace taken from the lower Fraser River.

Stomach analysis of collections taken between Hope and Chilliwack on September 3, 1960 showed that young-of-the-year were feeding exclusively on aquatic insect larvae, composed mostly of Diptera (90%). Yearling and adults collected at this time were feeding primarily on terrestrial insects composed exclusively of winged ants.

In October, November and March, only young-of-the-year were collected in the Fraser River between Hope and Chilliwack. These fish fed predominately on aquatic insect larvae, primarily Diptera.

REPRODUCTION

Gonad volume was used as an indication of sexual development and maturity. Volume determination was not attempted on fish of age 0 or I, nor on male fish of less than 80 mm fork length as the gonad volume was too small to be readily measured.

Gonad volume of age III and older female fish increased between June and July collections and was followed by a decrease between July and September collections. A similar increase and decrease was found among age III and older males of greater length than 80 mm. The decrease in gonad volume between July and September may be attributed to spawning. Young-of-the-year were first collected between August 16 and 18, 1960. These fish probably had hatched some two to three weeks previous to this collection date. Gonad development of maturing fish and the appearance of young-of-the-year suggests that the spawning period of leopard dace occurs early in July.

Some of the males of age III and older were found with a distinctive spawning colouration, as described by Carl *et al.* (1959). Not all males of this age group have such a colouration, but there was a higher percentage of coloured males of fork length greater than 80 mm. This colouration was observed in all seasons.

Age I male and female leopard dace are found with tubercles which occur on the dorsal surface of the head and body as well as the sides of the body, with exception of the fins. Gilbert and Everman (1895) refer to these as nuptial tubercles and claim they are also present on the dorsal surface of the pectoral fin rays. Tubercles on this area were not observed on fish from the Fraser River system.

COMPARATIVE ECOLOGY OF LEOPARD AND LONGNOSE DACE

Distribution in Water Current

Marked differences were noted in numbers of the two species taken in seine hauls made in slow and fast water current (Fig. 5). Differences were examined statistically with Chi-square tests, $P<0.05$ being the accepted level of significance.

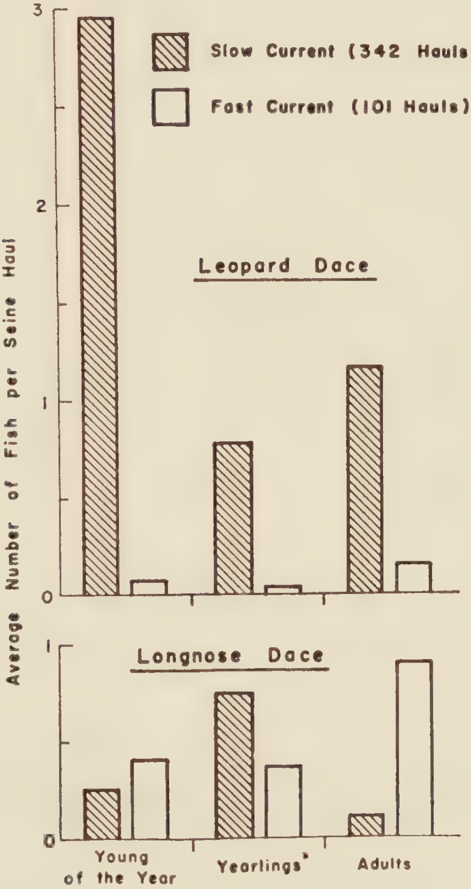

FIG. 5. Distribution of leopard and longnose dace in seine hauls made in slow (<0.5 m/sec) and fast (>0.5 m/sec) water currents throughout the lower and middle Fraser River system.

All age groups of leopard dace were taken in significantly greater numbers from hauls made in areas where water velocities were less than 0.5 m/sec. Although numbers of juvenile longnose dace were not significantly different between areas of slow and fast water current, the longnose dace apparently were more abundant in areas of fast current than were leopard dace. Adult longnose dace showed a significant "preference" for fast water current areas, the direct opposite of the response shown by leopard dace.

DEPTH DISTRIBUTION

In daylight (Fig. 6), young-of-the-year leopard dace were collected in greatest numbers in depths of less than 0.3 m while yearling fish of this species

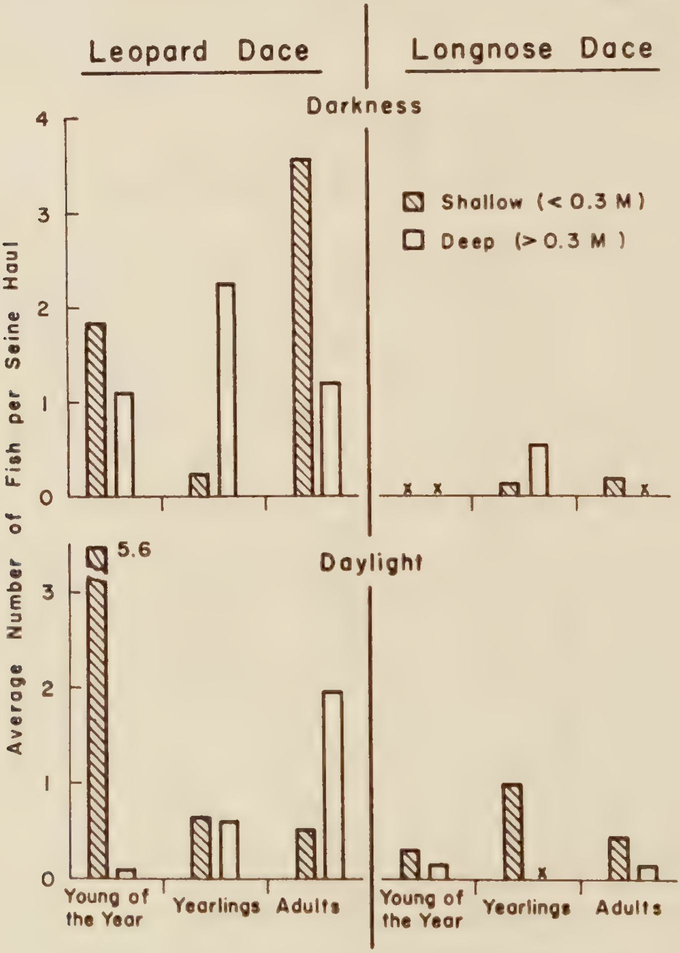

FIG. 6. Depth distribution of leopard and longnose dace during daylight and at night from all collection areas (X represents <0.1 fish/seine haul). In daylight, 135 hauls were in depths <0.3 m while 125 were >0.3 m; in darkness, 28 hauls were in depths <0.3 m while 27 were >0.3 m.

were collected with similar success in all depths up to the maximum seined (1 m). Adult leopard dace were collected most abundantly in depths of 0.3 – 1 m. All age groups of longnose dace were most commonly collected in depths less than 0.3 m. The results of 55 night seine hauls indicated that some juvenile leopard and longnose dace move offshore to depths greater than 0.3 m while adult leopard dace appear to move onshore and were collected in greater numbers in depths of less than 0.3 m. Adult longnose dace did not appear to show such movements.

Food of Juveniles

Stomach contents of leopard and longnose dace of age 0 and I, both collected from the same areas in the Fraser River between Hope and Chilliwack, are illustrated in Fig. 7. Both species of age 0 were collected together only in September and October, 1960. Diet of the two species was similar — both utilizing aquatic insect larvae as a major food source. Diptera larvae formed 96% (by volume) of the diet of leopard dace and 82% of longnose dace.

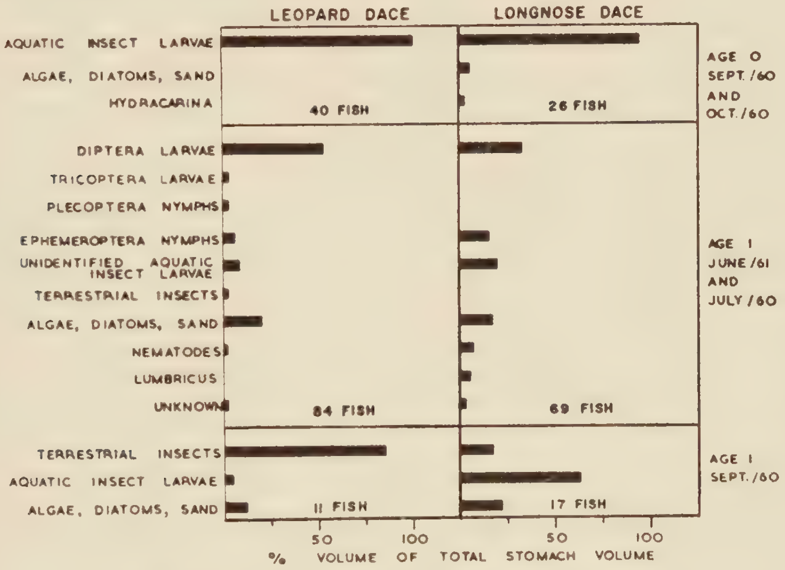

Fig. 7. Comparison of stomach contents of young-of-the-year and yearling leopard and longnose dace from the lower Fraser River.

Yearling fish (age I) of both species fed predominantly upon aquatic insect larvae during June 1961 and July 1960. Stomach analysis of yearling fish in September 1960 collections showed a change in diet; leopard dace switched to primarily terrestrial insects, while longnose dace continued to feed largely on aquatic insect larvae.

Current Preference in Experimental Stream

Laboratory experiments designed to test current preference indicated by field collections were completed on three size groups of both species of dace according to methods described previously.

Ratios of the number of leopard and longnose dace in the current arm (obtained by observation at hourly intervals) were analysed. The sum of the three experimental ratios of each size group at any given flow was called a block ratio.

Figure 8 illustrates the average number of fish in the current arm per observation. The vertical bars on this graph are proportional in area to the block ratios, thus avoiding difficulties of illustrating ratios with zero numbers.

The statistical procedure in the analysis of block ratios consisted of first a test of homogeneity on the 21 observed ratios composing the block ratio. Homogeneity was found in all block ratios. Homogeneity permitted a pooled Chi-square test to be calculated on the block ratios, $P < 0.05$ being the level of significance.

A significant difference was found between the numbers of longnose and leopard dace of the 70–95-mm size group at flows of 0.3, 0.6 and 0.9 m/sec. Longnose dace were more numerous in the current arm. The block ratio at the 1.2 m/sec velocity was not subjected to a Chi-square test as only one longnose dace was observed. Attempts to enter the current arm at this flow were observed during every other half-hour period throughout the three experiments. An attempt was recorded if a fish could swim up to the lip of the current arm ramp or further (Fig. 1). There was a significant difference in the number of attempts made by the two species to enter the current arm at the 1.2 m/sec velocity. Longnose dace made 53 attempts while leopard dace made only 18.

Significant differences were found between the two species (50–70-mm size) at velocities of 0.3 and 0.9 m/sec. Longnose dace again were more numerous in the current arm. At the 0.6 m/sec water velocity, longnose dace were more numerous, but the difference was not significant. At the 1.2 m/sec water velocity, one longnose dace was noted during three observations while leopard dace never entered the current arm. Attempts were not recorded for this size group.

Experiments were completed on the 30–40 mm size group at velocities of 0.3 and 0.6 m/sec. A significant difference between the species was found at 0.3 m/sec; longnose dace were more numerous in the current arm. No fish were observed in the current arm at 0.6 m/sec. Attempts, recorded at both velocities, showed that for every attempt made by leopard dace to enter the current arm, longnose dace made ten. This ratio, at both velocities, was significantly different.

In addition to the distribution of both species in the current arm of the stream tank, other observations in the area downstream from the partition and in the non-current arm (Fig. 1) clearly indicated the preference of longnose dace for areas of strong water current.

Swimbladder Volume

Except for the smallest individuals (young-of-the-year) compared, leopard dace have a swimbladder much larger than that of longnose dace (Fig. 9). Regression lines calculated for both species are significant ($P < 0.01$); the correlation coefficient (r) for leopard dace being 0.95 and that for longnose dace 0.30. In leopard dace the volume of the swimbladder increases sharply in heavier fish while that of longnose dace becomes only slightly larger in heavier individuals.

DISCUSSION

Although recently emerged fry (young-of-the-year) of both leopard and longnose dace were commonly taken together in relatively slow water velocities along the margin of a large river, divergence in habitat apparently begins early in their life. Some longnose dace fry were found in areas of higher water current within a few weeks after emergence while leopard dace fry were still most abundant in more quiet water. By the end of their first year the two species showed almost complete habitat divergence, leopard dace inhabiting slow moving regions of the river while longnose dace frequented riffles and other areas of distinct current.

Experiments in the stream tank on 30–40 mm fry which were approximately 8 months old showed a significant difference in current preference of the two species. Longnose dace fry had a much stronger current preference when compared to similar sized leopard dace (Fig. 8). In further experiments on response to water current of larger dace, the distinct preference of longnose dace for current was maintained and, in fact, leopard dace seemed unable to enter the current arm of the stream tank at water velocities of 0.9 or 1.2 m/sec while longnose dace frequently did so. The difference in current preference demonstrated experimentally between the two species may account for divergences in habitat observed in the field.

Habitat divergence of leopard and longnose dace after their first year is reflected in the diet of the two species. Longnose dace, moving into riffle areas with increased water current, continue to feed on aquatic insect larvae inhabiting such regions. On the other hand, yearling and older leopard dace, remaining largely in portions of the river with flow less than 0.5 m/sec, begin to feed heavily upon terrestrial insects when present. The latter might be more abundant and available to capture in regions of slow flow along the river margin.

Differences in volume of the swimbladder between the two species of dace appear to have significance in their choice of habitat. The principal function of the swimbladder is hydrostatic (Jones, 1957) and freshwater fish with well developed swimbladders comprising 7–10% of their total volume are able to swim easily in mid-water (Taylor, 1921; Jones, 1951). Both leopard and longnose dace have swimbladders occupying less than 7% of their total volume and thus may be better adapted for habitats near the bottom. However, it obviously would be advantageous for a bottom-dwelling fish inhabiting fast water areas of a stream to have as great a density as possible to maintain position. Nelson (1961) found that those genera of catostomids which are adapted to a riffle habitat (*Hypentelium*, *Thoburnia* and *Pantosteus*) have a reduced swimbladder volume when compared with other catostomids. The relatively low swimbladder volume of yearling and older longnose dace may be of considerable selective advantage in the occupation of such habitat. Swimbladder volumes of fry of both species are similar as are their habitats and food. As longnose dace increase in weight, the swimbladder volume shows little increase (Fig. 9), hence the density of the fish rises. This increase in density is paralleled by stronger preference for current in larger fish. On the other hand, the marked increase in swimbladder

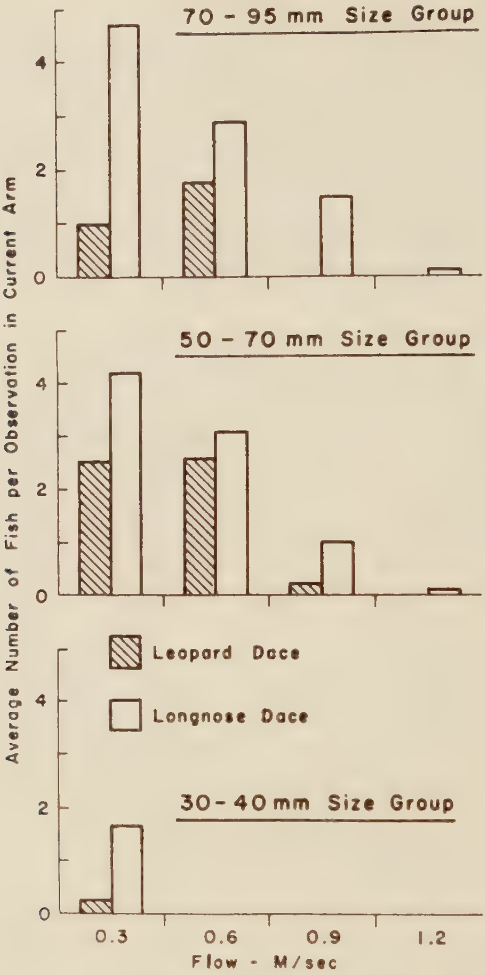

FIG. 8. Current preference of leopard and longnose dace in an experimental stream.

volume of yearling and adult leopard dace may be an adaptation to living in slow moving regions of stream margin, not in constant association with the bottom but feeding near or at the surface on terrestrial insects. Yearling and adult longnose dace have not been reported to feed to any extent on terrestrial insects (Johannes, 1958; Carl *et al.*, 1959).

Similar habitat and niche requirements of recently emerged leopard and longnose dace may be thought to oppose Gause's contention (Gause, 1934) that closely related species cannot coexist in the same niche without one species eliminating the other through competition. However, closely related species may coexist in a similar niche without effective competition in presence of a temporarily superabundant food (Lack, 1946; Hartley, 1953; Nilsson, 1960).

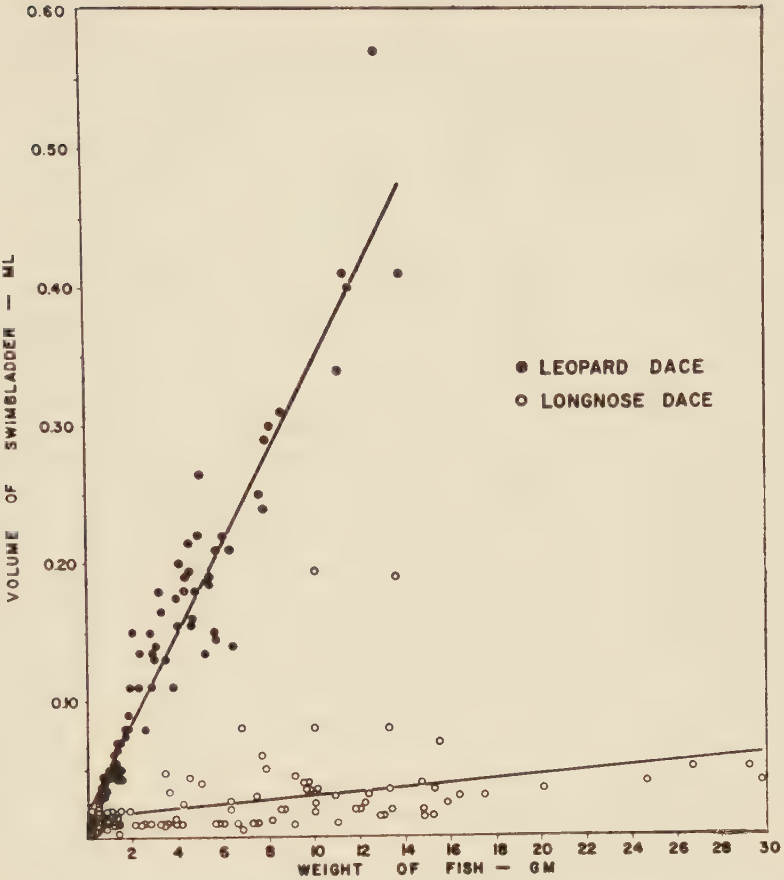

FIG. 9. Relationship between volume of swimbladder and weight of leopard and longnose dace from middle and lower Fraser River system.

In late July, the probable emergence period of both species, the Fraser River is still near its maximum annual discharge level. Part of the surrounding land of the lower Fraser Valley is flooded, providing large areas of slow or little current over low lying banks and gravel bars. These conditions combined with an increased food supply provided by flooding appear suitable to survival of recently emerged fish. Possibly at this time, with an excess of food and non-current areas, fry of the two species of dace could coexist in a similar niche. However, as the water level recedes in late summer and autumn such favourable environmental conditions for coexistence may become scarce resulting in increased interspecific competition during autumn and winter. As each species attempted to utilize its ecological potency (Kalleberg, 1958) and reduce the area of habitat overlap, increased divergence in habitat should occur. Nearly complete habitat divergence at the end of their first year may allow these two congeneric species which are found in the same river to live without entering into severe competition for those resources of the environment essential for their existence.

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Oceanography of the Subarctic Pacific Ocean[1]

By Michitaka Uda[2]

Fisheries Research Board of Canada
Pacific Oceanographic Group, Nanaimo, B.C.

ABSTRACT

All available oceanographic data observed from 1951 through 1958, north of Lat. 35° N in the Pacific Ocean, the Sea of Okhotsk, and the Bering Sea, together with the relevant literature, were examined. There were sufficient data from 1955 through 1958 to prepare composite charts of salinity, temperature, dissolved oxygen and transparency of the near-surface waters in the Subarctic Region from Asia to America.

The Subarctic Pacific is defined as the region in which there is a marked halocline separating a low salinity upper zone from a more saline lower zone. It includes all areas having dichothermal temperature structure. Definite boundaries for the region are established. The Subarctic characteristics are limited to the upper zone and halocline. The lower zone characteristics are continuous from the Subtropic into the Subarctic.

From the data the principal features of structure of the properties have been shown, as well as the differences from one locality to another. The seasonal variations and also some non-seasonal variations have been discussed. The persistent current systems have been traced and their components named.

The processes for the maintenance of the structure by precipitation, evaporation, dissipation of upper zone water, and entrainment from the deep zone are discussed. A relation between the barometric pressure distribution and the transport in the non-persistent current systems is proposed.

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[1] Received for publication June 19, 1962.

[2] Author's present address: Tokyo University of Fisheries, 6 Chome, Shiba Kaigan Dori, Minato-ku, Tokyo, Japan.

J. Fish. Res. Bd. Canada, **20**(1), 1963.
Printed in Canada.

A. INTRODUCTION

THIS PAPER constitutes an attempt to present a concise but comprehensive review of the oceanography of what will be termed the Subarctic Pacific Oceanic Region. The term "region" will be considered to represent an oceanic area which is characterized generally throughout by one or more oceanographic features peculiar to the area. The Subarctic Pacific possesses features not found in any other region.

It is hoped that this report will serve a two-fold purpose: firstly, as a primer of the oceanographic knowledge that has been gained in the region up to the present time (1959) and secondly, as a guide for those whose interests are directed toward the various facets of the major fisheries of the area. With respect to the latter, a knowledge of the basic oceanographic features is a necessary prerequisite for any significant work on such aspects as the migration patterns and the feeding characteristics of commercially-significant fishes.

B. THE SUBARCTIC REGION

1. GEOGRAPHY

Figure 1 shows the Subarctic Region as defined in this paper, including all geographical terms used. The region involved is basically triangular in shape. At its northern apex (Lat. 66° N) is the narrow (31 miles or 58 km) and shallow (30 fathoms or 58 m) Bering Strait. To the south, the boundary is the northern limit of the Polar Front Region (page 127). This boundary lies on the Great Circle route from Tokyo to Los Angeles. In mid-ocean it lies generally between Lat. 40° and 45° N. The coast of North America forms the eastern boundary of the region. Along the western boundary lie the northern Japanese islands, the Okhotsk Sea and the Siberian coast. The Okhotsk Sea is roughly rectangular in shape, and is bounded on three sides by the Siberian coast (including the Kamchatka Peninsula). Access by water to the Okhotsk is possible only at the south side and is limited by the Kurile Island Chain. Access to the Bering Sea is influenced in a similar manner by the Aleutian Island Chain, the southern boundary of that sea.

2. BATHYMETRY

It is to be noted that this and the following section have drawn heavily upon information given by Fleming (1955). This information is included in the present work for the sake of completeness.

The bathymetry of the region (Fig. 1) is notable for the marked contrasts in depth. The greatest depths, those exceeding 4000 fathoms (about 7300 m), are found in deep trenches that lie parallel to the island chains. By contrast, the northern and eastern parts of the Bering Sea, and much of the northern Okhotsk Sea, overlie the continental shelf. The shelf is represented approximately by the area between the coast and the 100-fathom (about 200 m) contour. These parts of the Bering Sea are extremely shallow, possessing a maximum depth of only about 30 fathoms (55 m). Basins having depths of about 1750 fathoms (3200 m), intermediate to the extremes just noted, are present in both the Okhotsk and southern Bering Seas. The remainder of the region is essentially an abyssal plain, averaging about 2500 fathoms (about 4500 m). In the northeastern Subarctic, several chains of seamounts are present. Some of the seamounts rise to within 400 fathoms (about 730 m) of the surface.

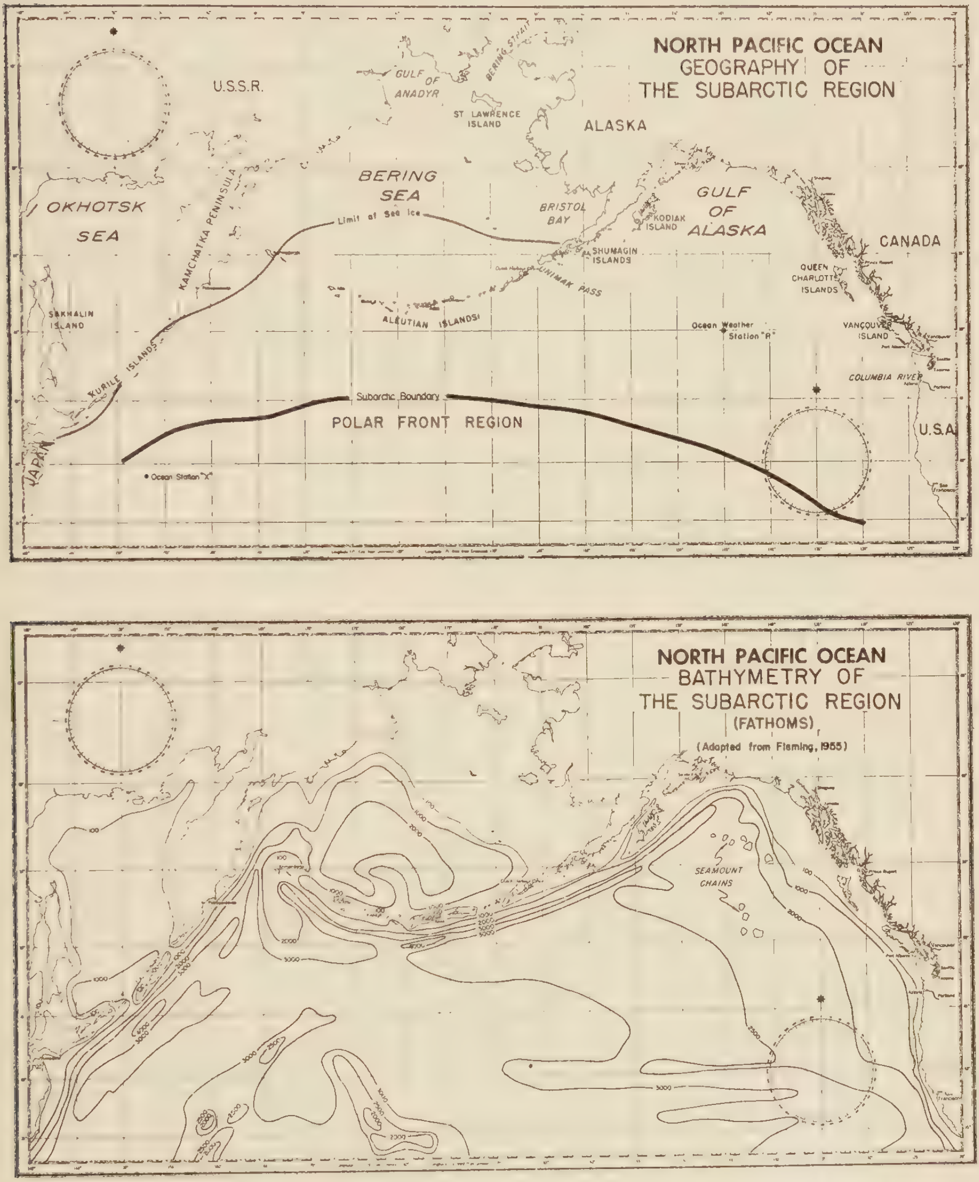

NORTH PACIFIC OCEAN
GEOGRAPHY OF
THE SUBARCTIC REGION
U.S.S.R.
GULF OF ANADYR
BERING STRAIT
ST LAWRENCE ISLAND
ALASKA
BERING SEA
OKHOTSK SEA
KAMCHATKA PENINSULA
Limit of Sea Ice
BRISTOL BAY
KODIAK ISLAND
GULF OF ALASKA
SHUMAGIN ISLANDS
UNIMAK PASS
CANADA
QUEEN CHARLOTTE ISLANDS
SAKHALIN ISLAND
ALEUTIAN ISLANDS
Ocean Weather Station "P"
VANCOUVER ISLAND
COLUMBIA RIVER
KURILE ISLANDS
Subarctic Boundary
POLAR FRONT REGION
JAPAN
U.S.A.
Ocean Station "X"
NORTH PACIFIC OCEAN
BATHYMETRY OF
THE SUBARCTIC REGION
(FATHOMS)
(Adapted from Fleming, 1955)
SEAMOUNT CHAINS
1000
2000
3000
2500

FIG. 1. Geography and Bathymetry (fathoms) of the Subarctic Region (adapted from Fleming, 1955).

3. Climatology

(i). Winds. During the winter (December to early April) the Subarctic Pacific Region is usually under the influence of a low-barometric pressure cell centred in the area of the Bering Sea and the Aleutian Islands (the Aleutian Low) (Fig. 2). Coincident with this, two high-pressure cells (the Siberian and the North American Arctic High) occur. Under the influence of these cells the winds in winter (Fig. 2) are generally westerly; they blow from the northwest in the western part of the region, gradually turning through southwest in the

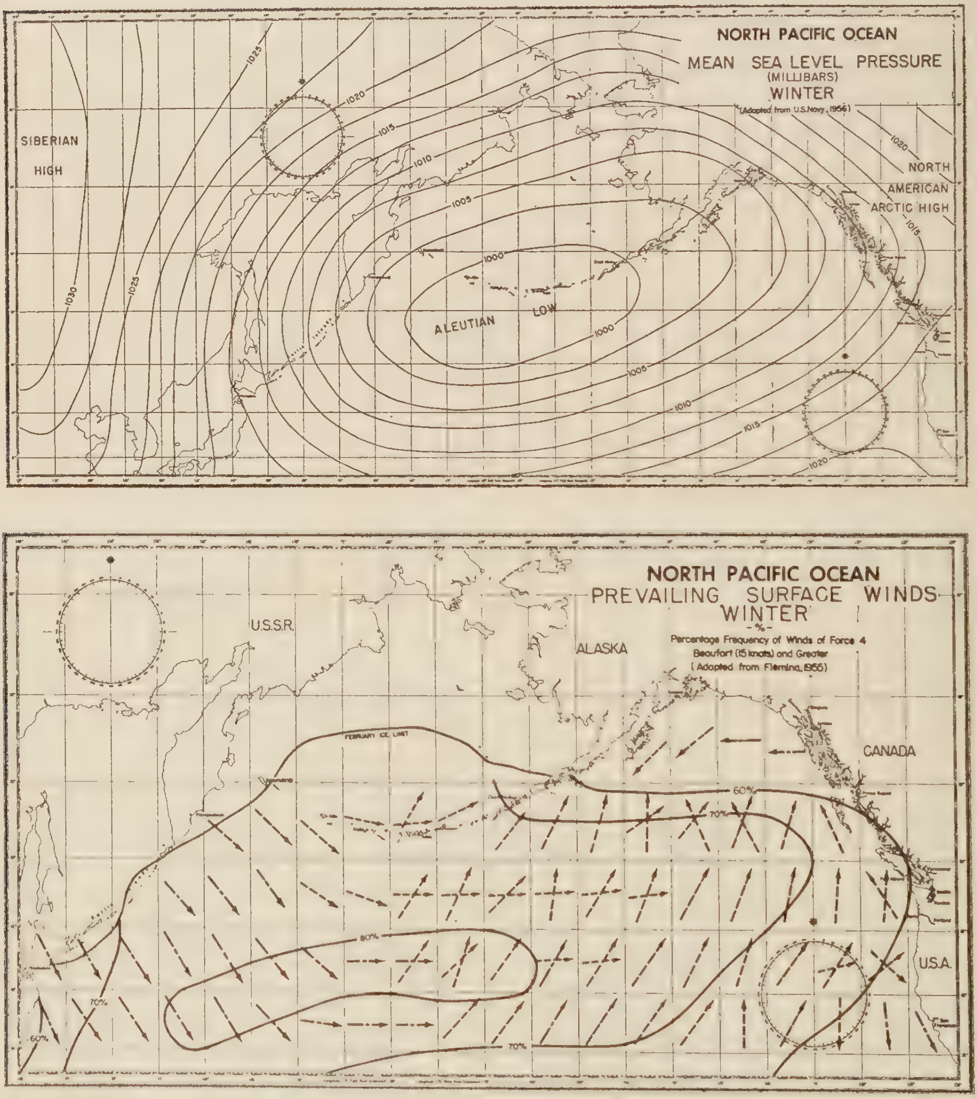

NORTH PACIFIC OCEAN
MEAN SEA LEVEL PRESSURE
(MILLIBARS)
WINTER
(Adapted from U.S.Navy, 1956)
SIBERIAN HIGH
NORTH AMERICAN ARCTIC HIGH
ALEUTIAN LOW
1030
1025
1020
1015
1010
1005
1000
NORTH PACIFIC OCEAN
PREVAILING SURFACE WINDS
WINTER
-%-
Percentage Frequency of Winds of Force 4 Beaufort (15 knots) and Greater
(Adapted from Fleming, 1955)
U.S.S.R.
ALASKA
CANADA
U.S.A.
FEBRUARY ICE LIMIT
60%
70%
80%

Fig. 2. Mean Sea Level Pressure (millibars), Winter (adapted from U.S. Navy, 1956) and Prevailing Surface Winds, Winter (adapted from Fleming, 1955).

central and eastern Pacific. In the northern part of the Gulf of Alaska, easterly winds prevail.

In early summer (Fig. 3) the Aleutian Low vanishes and the North Pacific High, centred between about Lat. 30° and 40° N, becomes predominant. The prevailing westerlies of the winter months are then replaced by the predominately south or southwest winds (Fig. 3). These warm southerly winds cause extensive

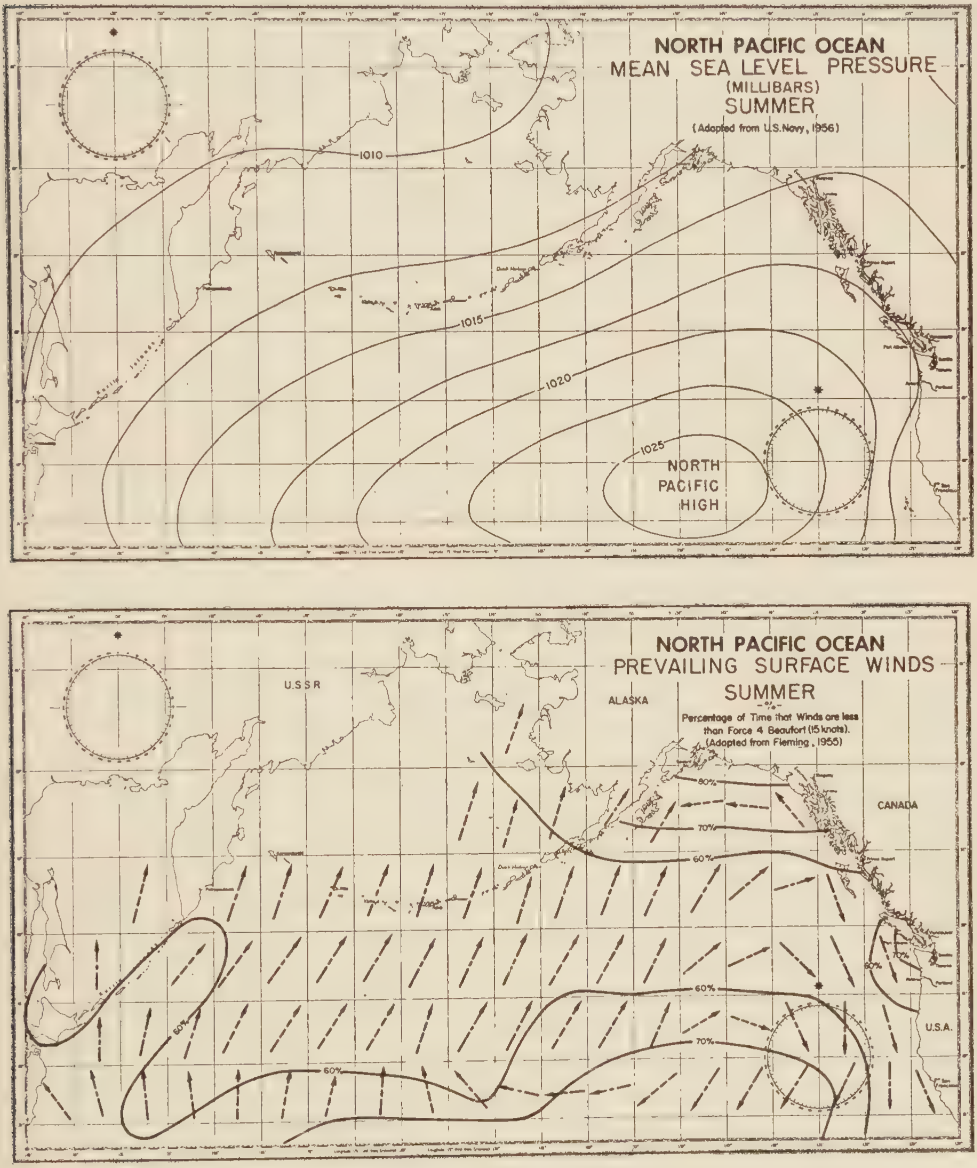

NORTH PACIFIC OCEAN
MEAN SEA LEVEL PRESSURE
(MILLIBARS)
SUMMER
(Adopted from U.S.Navy, 1956)
1010
1015
1020
1025
NORTH PACIFIC HIGH
NORTH PACIFIC OCEAN
PREVAILING SURFACE WINDS
SUMMER
-%-
Percentage of Time that Winds are less than Force 4 Beaufort (15 knots).
(Adopted from Fleming, 1955)
U.S.S.R
ALASKA
CANADA
U.S.A.
80%
70%
60%
60%
70%
60%
70%
60%
60%
70%

FIG. 3. Mean Sea Level Pressure (millibars), Summer (adapted from U.S. Navy, 1956) and Prevailing Surface Winds, Summer (adapted from Fleming, 1955).

"advection" fogs during their passage over the cold waters off Kamchatka and the Aleutian Chain. On the eastern side of the Subarctic Region (off the Canadian and U.S. coasts) the dominant summer winds are from a northwest direction. Light variable winds occur in the Gulf of Alaska at this time.

(ii). PRECIPITATION. It has been shown (Jacobs, 1951) that precipitation exceeds evaporation throughout the year over essentially the entire Subarctic Pacific Region. The mean values for the excess in winter, in summer and throughout the year are shown in Fig. 4. It will be noted that the maximum excess always occurs in the eastern portion, off the North American coast, where land drainage enhances the effect. Appreciable runoff occurs north of Lat. 45° N on both the eastern and western sides of the region. In sum, the Subarctic Pacific is a region of net dilution.

(iii) SEA ICE. Starting usually in October sea ice spreads rapidly southward; the maximum extent of the ice usually occurs in February of each year, and is shown in Fig. 1. During the winter, ice is present throughout the northern half of the Bering Sea and covers the entire Sea of Okhotsk. By early July, it is found only in the Gulf of Anadyr and in Bering Strait. In late July and August, all ice has effectively disappeared from the region, and open water is present to the north of the Strait.

C. PREVIOUS WORK

The results of oceanographic research to about 1940 in the North Pacific Ocean (which includes the Subarctic Region) have been examined in some detail by Sverdrup *et al.* (1942). Fleming (1955) summarized the basic features of the oceanography of the Northern Pacific from data available up to and including 1954.

The scope of the investigations in the Subarctic was greatly expanded in the summer of 1955 when research agencies of Japan, Canada and the United States carried out detailed surveys in particular areas which were coordinated to provide quasi-synoptic coverage of the ocean north of Lat. 20° N. This program was referred to as NORPAC. In succeeding years, several summer and winter surveys have been carried out in the eastern part of the region by Canada. In addition, oceanographic data have been obtained during extensive exploratory fishing cruises carried out every summer by Japan and the United States. Comprehensive oceanographic observations have also been made at Ocean Weather Station "P" (Lat. 50° N, Long. 145° W) since late in 1956. The presence of many of the representative oceanographic features of the Subarctic Region have been made strikingly evident from these "time-series" studies at Station "P".

It is on the data obtained during and subsequent to Project NORPAC that this paper is primarily based. The sources of the data are appended.

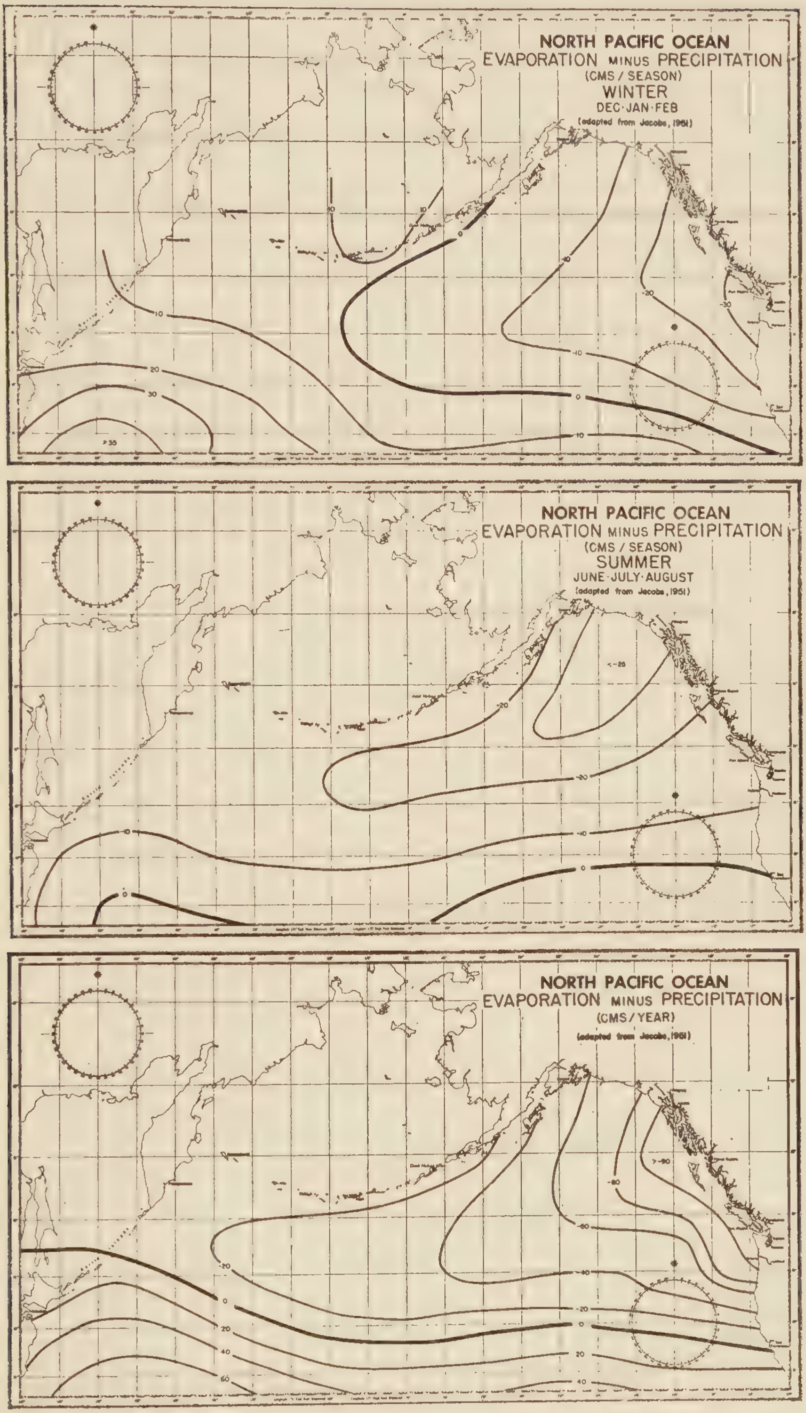

NORTH PACIFIC OCEAN
EVAPORATION MINUS PRECIPITATION
(CMS / SEASON)
WINTER
DEC·JAN·FEB
(adapted from Jacobs, 1951)
10
10
0
10
20
30
>35
-10
-20
-30
-10
0
-10
NORTH PACIFIC OCEAN
EVAPORATION MINUS PRECIPITATION
(CMS / SEASON)
SUMMER
JUNE·JULY·AUGUST
(adapted from Jacobs, 1951)
<-25
-20
-20
-10
10
0
0
NORTH PACIFIC OCEAN
EVAPORATION MINUS PRECIPITATION
(CMS / YEAR)
(adapted from Jacobs, 1951)
>-90
-80
-60
-40
-20
-20
0
0
20
20
40
60
40

FIG. 4. Evaporation minus precipitation, winter (cms/season), summer (cms/season), and annual (cms/year) (adapted from Jacobs, 1951).

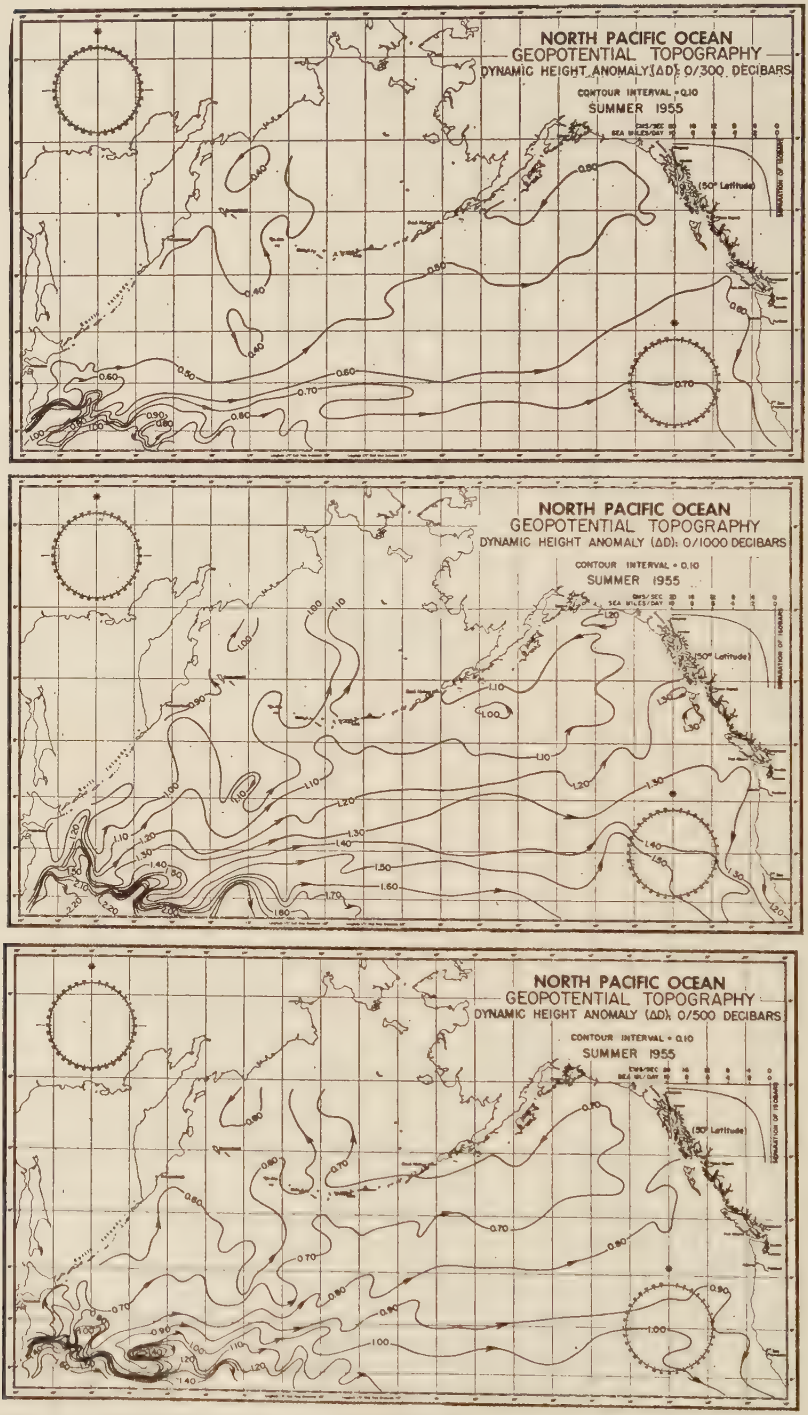

NORTH PACIFIC OCEAN
GEOPOTENTIAL TOPOGRAPHY
DYNAMIC HEIGHT ANOMALY (ΔD): 0/300 DECIBARS
CONTOUR INTERVAL = 0.10
SUMMER 1955
(50° Latitude)
NORTH PACIFIC OCEAN
GEOPOTENTIAL TOPOGRAPHY
DYNAMIC HEIGHT ANOMALY (ΔD): 0/1000 DECIBARS
CONTOUR INTERVAL = 0.10
SUMMER 1955
(50° Latitude)
NORTH PACIFIC OCEAN
GEOPOTENTIAL TOPOGRAPHY
DYNAMIC HEIGHT ANOMALY (ΔD): 0/500 DECIBARS
CONTOUR INTERVAL = 0.10
SUMMER 1955
(50° Latitude)

FIG. 5. Geopotential topography — 0/300, 0/500 and 0/1000 decibars, summer 1955.

D. THE PERSISTENT CURRENT SYSTEM IN THE SUBARCTIC PACIFIC REGION

Figure 5 shows the geopotential topography of the Subarctic Region referred to the 300-, 500-, and 1000-decibar surfaces respectively. The data were collected during the summer of 1955 (the period of most intensive coverage of the region). Also, the topography referred to the 1000-decibar surface is shown for each summer from 1956 through 1958 (Fig. 6). The currents are presumed to flow along the isobaths with a speed inversely proportional to the spacing between isobaths.

The more important components of the persistent circulation in the upper layers in the Subarctic Pacific (as deduced from recurrent features in these charts of geopotential topography) are shown and named in Fig. 7.

A cold southward-moving current of low salinity, the Oyashio, is present along the eastern side of the Kurile Islands and along the northern Japanese island (Uda, 1938a, b). The warm, saline Kuroshio moves northeastward off the Japanese islands to about Lat. 40° N. This current is relatively swift, especially at the surface, having a speed of the order of one knot (50 cm/sec) or more. At the confluence of the two currents, extensive mixing occurs both horizontally and vertically. The area is usually characterized by a widespread system of eddies. The mixed water, and most of the remainder of the two currents, turn eastward as the "West Wind Drift". This has a much slower speed than the Kuroshio, moving at the rate of about 2–4 nautical miles/day (4–8 cm/sec). The speed is relatively uniform to a depth of at least 300 m.

The mixed water constitutes the Polar Front, which is a transitional region about 2° to 4° of latitude in width; the location varies across the Pacific (Kawai, 1955; Uda, 1938a, b). To the north of the Front, the water is termed Subarctic (the region of primary interest to this paper), while to the south it is termed Subtropic. In the Front there is a marked gradation of oceanographic properties, from those typical of the one region to those typical of the other.

Off the American coast, the West Wind Drift (which has become progressively more dilute because of precipitation) divides. In the region of separation, the currents are weak and variable (Doe, 1955). The Subtropic water, the Polar Front water, and part of the Subarctic water turn south to form the California Current which flows toward the tropics and eventually joins the North Equatorial Current. The remainder of the Subarctic water is deflected northward and circulates around the Gulf of Alaska. The dynamic centre of this cyclonic circulation is termed the Alaska Gyre. This centre varies in position from 200–300 miles south of Kodiak Island (Fig. 1, 5 and 6).

Between the Gyre and the Alaskan coast the circulation both narrows and accelerates, reaching speeds of about 4–6 miles per day (8–12 cm/sec). From Kodiak Island to Unimak Pass the current is termed the Alaska Stream (Schott, 1935; Bennett, 1959), and beyond Unimak, the Alaska Stream Extension (page 168). The water is relatively warm and, especially in summer, becomes progressively more diluted as it moves westward. The near-surface layers finally enter the Bering Sea through the Aleutian passes nearest the Alaskan

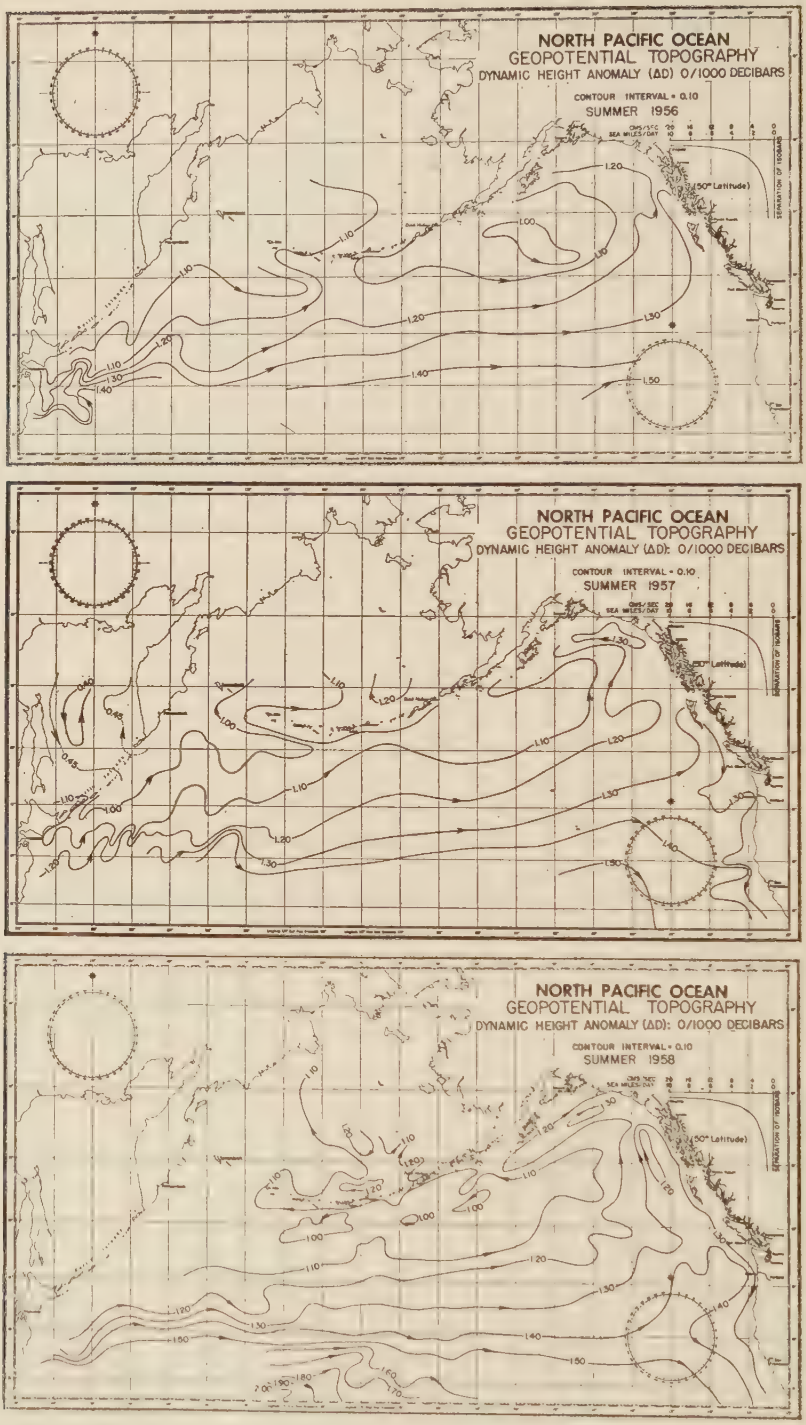

NORTH PACIFIC OCEAN
GEOPOTENTIAL TOPOGRAPHY
DYNAMIC HEIGHT ANOMALY (ΔD) 0/1000 DECIBARS
CONTOUR INTERVAL = 0.10
SUMMER 1956
CMS/SEC
SEA MILES/DAY
(50° Latitude)
SEPARATION OF ISOBARS
1.20
1.00
1.10
1.30
1.40
1.50
NORTH PACIFIC OCEAN
GEOPOTENTIAL TOPOGRAPHY
DYNAMIC HEIGHT ANOMALY (ΔD): 0/1000 DECIBARS
CONTOUR INTERVAL = 0.10
SUMMER 1957
1.30
1.10
1.20
1.00
0.40
0.45
1.40
1.50
NORTH PACIFIC OCEAN
GEOPOTENTIAL TOPOGRAPHY
DYNAMIC HEIGHT ANOMALY (ΔD): 0/1000 DECIBARS
CONTOUR INTERVAL = 0.10
SUMMER 1958
1.10
1.20
1.00
1.30
1.40
1.50
1.60
1.70
1.80
1.90
2.00

FIG. 6. Geopotential topography — 0/1000 decibars, summer 1956, summer 1957 and summer 1958.

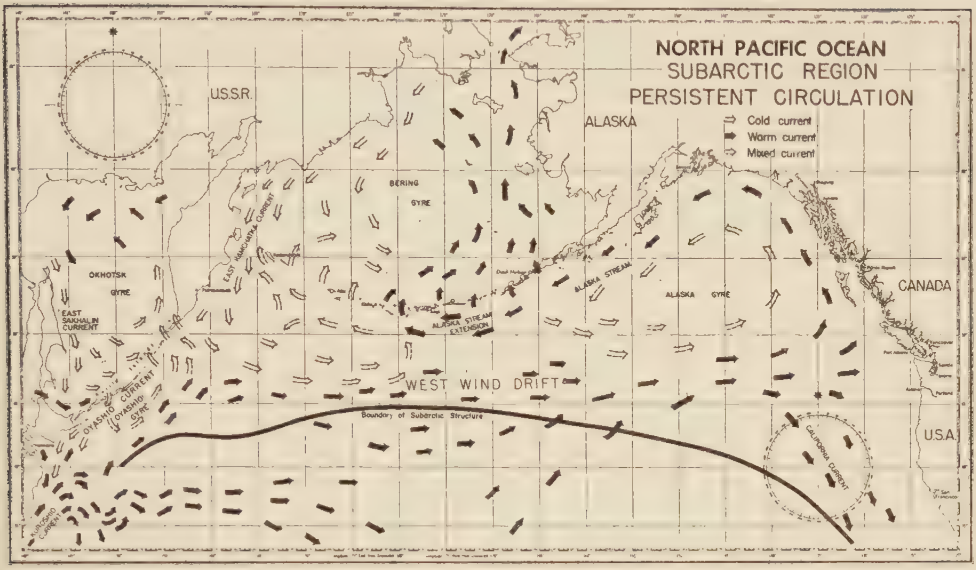

NORTH PACIFIC OCEAN
SUBARCTIC REGION
PERSISTENT CIRCULATION
⇒ Cold current
➡ Warm current
⇒ Mixed current
U.S.S.R.
ALASKA
CANADA
U.S.A.
BERING GYRE
OKHOTSK GYRE
EAST SAKHALIN CURRENT
EAST KAMCHATKA CURRENT
OYASHIO CURRENT
OYASHIO GYRE
KUROSHIO CURRENT
ALASKA STREAM EXTENSION
ALASKA STREAM
ALASKA GYRE
WEST WIND DRIFT
Boundary of Subarctic Structure
CALIFORNIA CURRENT

FIG. 7. Persistent circulation in the Subarctic Region.

mainland. The deeper waters move through the deeper passages which lie farther to the west.

The water in the Bering Sea moves in a cyclonic path. Some passes east of St. Lawrence Island and moves through Bering Strait. Observations in the Strait indicate that the flow through it is predominantly northward (Goodman *et al.*, 1942). Of the remainder, which turns southward along the Siberian coast, one part (modified by climatic conditions in the immediate area) becomes the East Kamchatka Current. The other part is absorbed into the cyclonic Bering Gyre which appears to be present in the Bering Sea.

In turn, part of the East Kamchatka Current moves into the Okhotsk Sea through passages in the North Kurile Island Chain, is modified, and circulates in a cyclonic path. On the western side of the sea it becomes the East Sakhalin Current. Most of this current moves out through the middle Kurile passages to form, with the East Kamchatka Current, part of the cold Oyashio (page 167). A portion remains in the (cyclonic) Okhotsk Gyre.

The circulation in the Subarctic Pacific is closed, aside from the water lost from the system through the Bering Strait to the Arctic Ocean, and through the California Current to the Subtropic Region. It appears that about 6 years are necessary for the round trip (Tully and Barber, 1960).

This picture of the persistent currents has been deduced from summer data. Confirmation of its major features has come, in the eastern part of the region at least, from geopotential topography derived from winter data (Dodimead, 1958) and from the results of drift-bottle releases (Dodimead and Hollister, 1958).

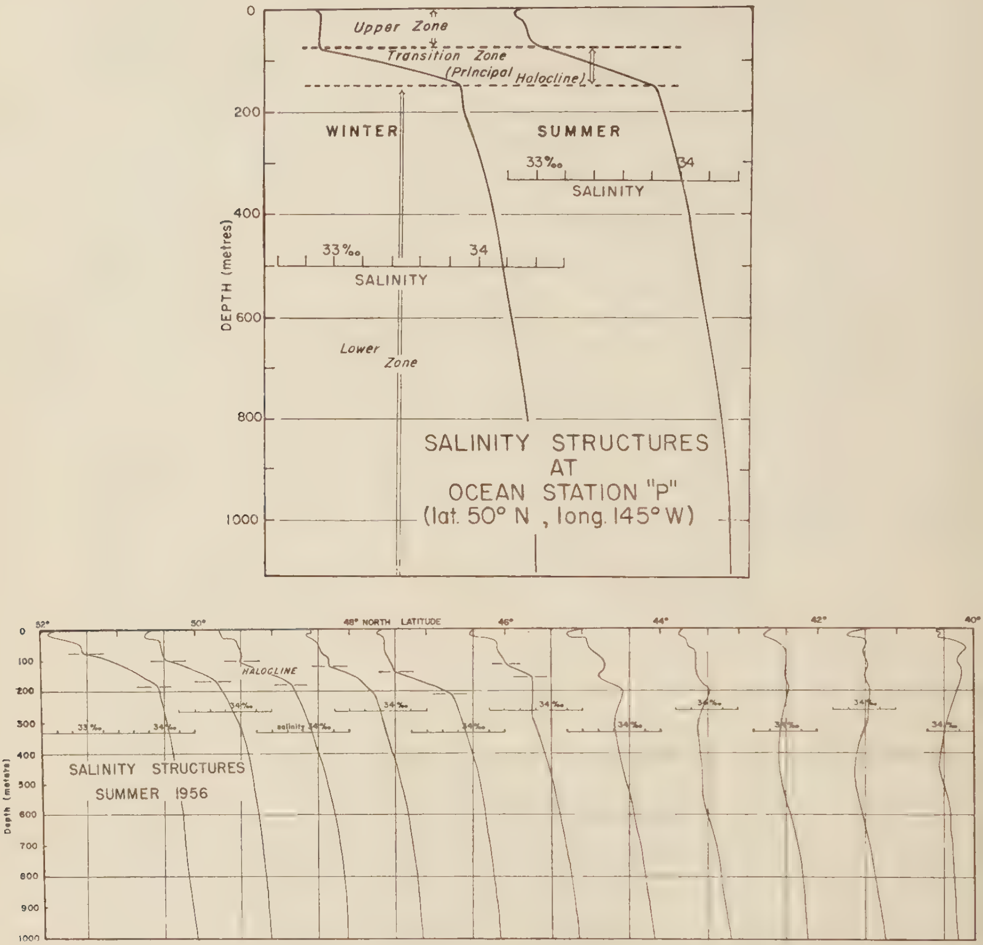


FIG. 8. Salinity structures at Ocean Station "P", winter and summer and in a north–south section in mid-Pacific Ocean.

E. SALINITY OF SUBARCTIC WATERS

It has been found that the most effective method of defining Subarctic waters is by a description of the *structure*, which term here denotes the variation of seawater properties in a *vertical* column or section. On the basis of structure (primarily that of salinity, but also to a lesser degree, that of temperature) the north Pacific can be divided into three distinctly separate regions. Each region is characterized by a different structure, each structure in turn possessing the same general characteristics throughout a region. The three are — in order of decreasing latitude — the Subarctic, the Polar Front, and the Subtropic (Fig. 1). As befits the title of this paper, the structure found in the first will be discussed in detail. A few salient features of the remaining regions will be noted, for purposes of general comparison.

1. SALINITY STRUCTURE

In the Subarctic Region, the salinity structure is in general characterized by three well-defined zones, an *upper*, a *transition* (*principal halocline*), and a *lower* zone. Typical salinity profiles which reveal the vertical extent of the zones in both winter and summer are depicted in Fig. 8.

The upper zone is generally of low salinity throughout the year, values usually being less than 33‰. At all times, the lowest values are present near the North American coast, where land drainage augments the excess of precipitation over evaporation (Fig. 4).

The characteristics of the salinity–depth profile have been discussed by Dodimead (1961). The profile changes from summer to winter. In the winter the upper zone is near-isohaline and is about 100 m in depth. This condition presumably results from complete mixing associated with convection due to surface cooling and with storms prevalent in the Subarctic at that time. During the summer period, the salinity structure in the upper zone is somewhat more complicated. There is a near-isohaline layer which extends to a depth of from 10–30 m. This layer presumably represents the effect of mixing associated with the lighter winds generally present in the region in summer. Then there occurs a small halocline followed by another near-isohaline layer to a depth, in the open ocean, of about 100 m.

Below this upper zone (Tully and Barber, 1960) there exists throughout the year, the *transition zone* or *principal halocline*. In this zone the salinity increases by about 1‰ from 100 to 200 m depth. The bottom of this halocline can be defined to a high degree of accuracy (±0.1‰) throughout the Subarctic Region by the isohaline surface of salinity 33.8‰. Below this, in the so-called *lower zone*, the salinity increases gradually (by about 0.6‰) but uniformly in the next 1000 m, and even more gradually (by about 0.2‰) in the succeeding 1000 m. It is found that, in the lower zone, surface-induced (seasonal) variations in the oceanographic properties are negligible (Tully *et al.*, 1960). Changes of properties in this zone must therefore be due primarily to advective effects.

Dodimead (1961) has shown that the "three-zone" structure is characteristic of the mid-ocean portion of the Subarctic Region. However, it is not present in all coastal areas. In localities where intense mixing occurs because of topographical features, such as in the passes of the Aleutian Island Chain, the upper boundary of the halocline may be as deep as 400 m and the lower boundary may be indefinite. This represents the greatest depth at which the halocline has been found. It is shallowest in summer in areas such as the Bering and Okhotsk Seas, where sea ice is formed in winter. No halocline is present in winter in the shallow (i.e. the northern and eastern) portions of the Bering Sea. Convective overturn associated with sea-ice formation renders the water isohaline from surface to bottom. Isohaline conditions are present effectively throughout the year near the southern edge of the continental shelf in the Bering Sea (Fig. 1). These conditions may have their origin in the mixing occurring over the shallow bottom in that area. The lower diagram of Fig. 8 (Dodimead, 1961) illustrates the sequence of structures along a north–south section between 165° and 175°

west longitude. This section extends from the Subarctic through the Polar Front into the Subtropic Region in mid ocean.

The term "Polar Front" usually has the connotation of a zonal belt in which there is a marked meridional temperature gradient. This occurs generally between 40° and 45° N in the north Pacific Ocean. There is a corresponding marked change of salinity through this belt, at least in mid-ocean; hence the term Polar Front is used here to designate the transition belt in both salinity and temperature structures.

Southward through the Polar Front, the halocline becomes progressively less distinct (Dodimead, 1961). At the southern side of the belt, the structure becomes effectively isohaline to a depth of several hundred metres. Surface salinities increase to about 33.8‰ through the Front to the southern edge. As many as three salinity inversions may be found in the upper 150 m or so, but temperature considerations (page 147) indicate that these can be density-stable. Considerable fluctuations in salinity structure, both in space and time, occur in this transition belt.

In the Subtropic Region, south of the Polar Front, the salinity structure is marked throughout the year by high surface values (greater than 34‰) and by a decrease of salinity with depth to a minimum at 300–800 m. No marked halocline is present in this region. The high surface salinity is a consequence of the excessive evaporation (Fig. 4) due to the prevailing Westerlies (Fig. 2 and 3).

The salinity and structure in the deep water, below the salinity minimum and the halocline, are similar and continuous from the Subtropic through the Subarctic.

2. Horizontal Distribution of Salinity

Summer and winter horizontal distributions of surface-layer salinities, during the years 1955 through 1958 inclusive are shown, to the extent of the data available, in Fig. 9 through 13. It appears that distributions at the surface and at 10 m depth in the Subarctic both present the same basic features (compare Fig. 9, 10 with 11, 12). It is believed, however, that conditions at 10 m are most nearly representative of the prevailing seasonal state. Presumably those at the surface would be more influenced by transient effects, (evaporation, dilution, etc.) especially in the summer periods. In winter, conditions at the two levels would presumably be practically identical, because of the strong convection and wind mixing. It was found possible to draw similar conclusions with respect to both temperature and dissolved oxygen distributions. Therefore, throughout the remainder of this paper, surface-layer conditions will be represented by the data from 10 m depth.

In the surface-layer salinity pattern, several permanent features are noticeable. The trend of the isohalines appears to be basically east–west throughout the year. Marked modifications, however, occur along the shoreline and are attributable to the current systems, coastal winds and land drainage. A permanent salinity maximum is present in the Gulf of Alaska, south of Kodiak Island. Maxima have also been observed to occur in both the southern Bering

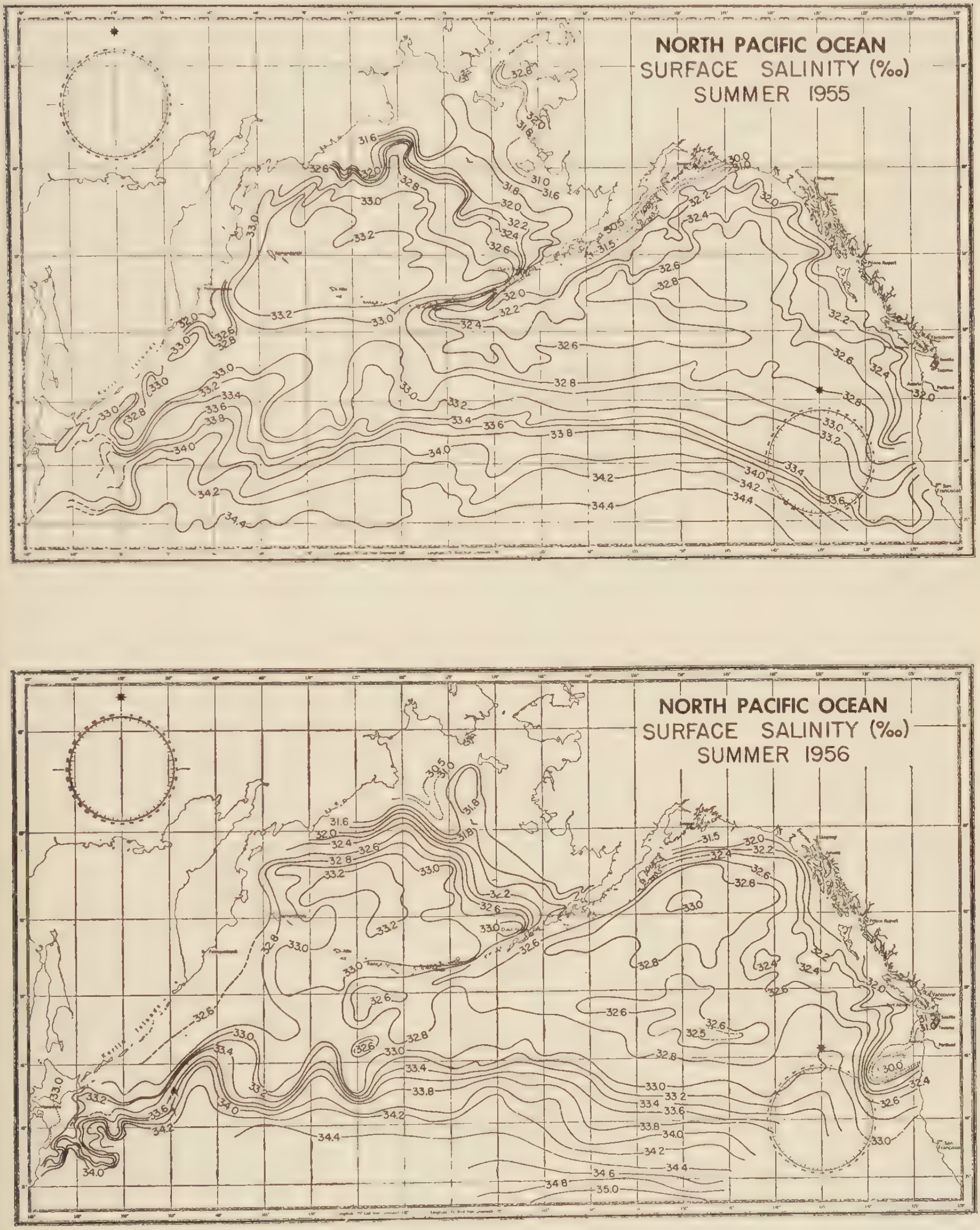

NORTH PACIFIC OCEAN
SURFACE SALINITY (‰)
SUMMER 1955
31.6
32.6
32.0
32.8
33.0
33.2
31.8
31.0
32.2
32.4
30.0
30.5
31.5
33.4
33.6
33.8
34.0
34.2
34.4
NORTH PACIFIC OCEAN
SURFACE SALINITY (‰)
SUMMER 1956
30.5
31.0
31.6
31.8
31.5
32.0
32.2
32.4
32.6
32.8
33.0
33.2
33.4
33.6
33.8
34.0
34.2
34.4
34.6
34.8
35.0
32.5
30.0

FIG. 9. Surface salinity, summer 1955 and summer 1956.

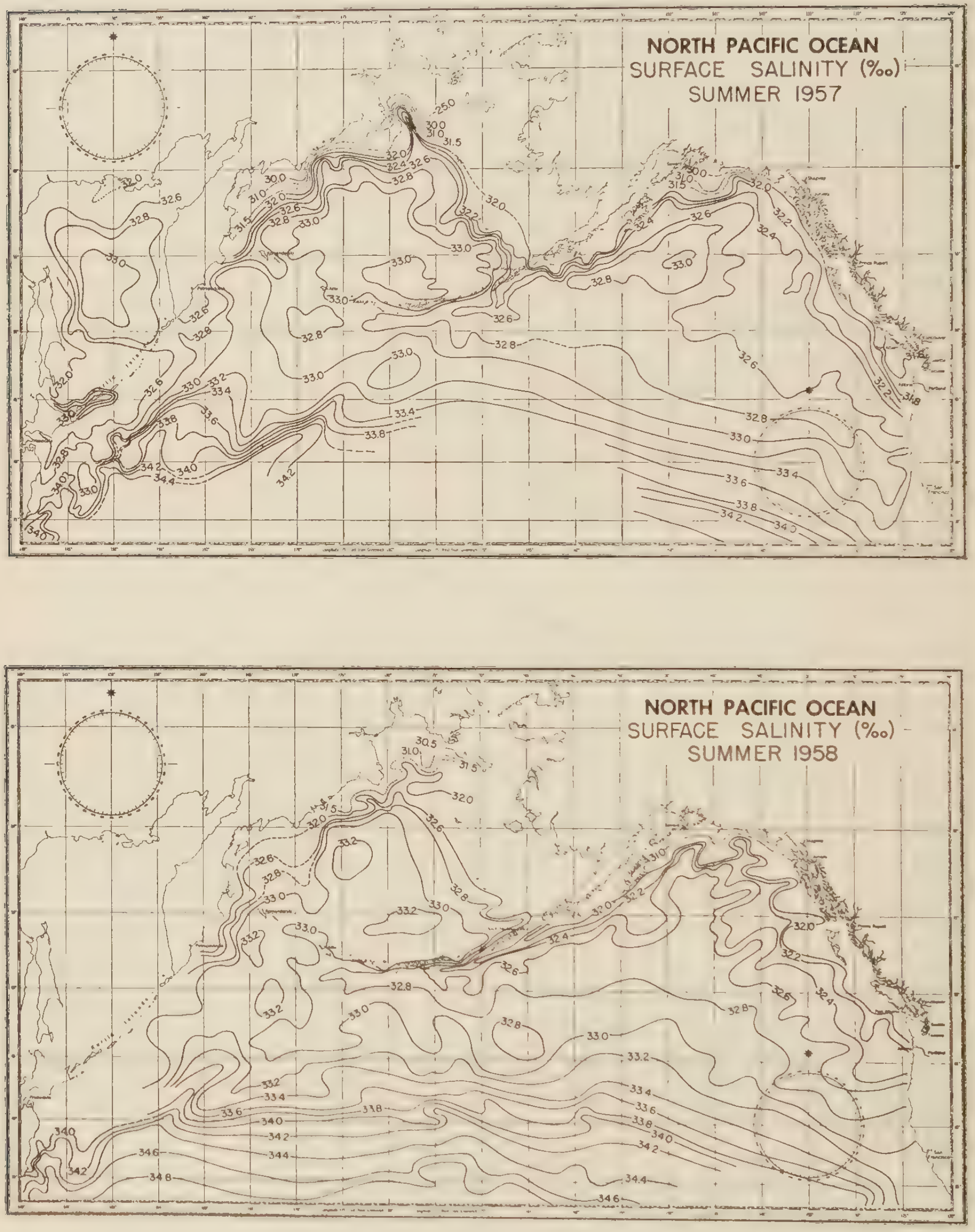

NORTH PACIFIC OCEAN
SURFACE SALINITY (‰)
SUMMER 1957
25.0
30.0
31.0
31.5
32.0
32.2
32.4
32.6
32.8
33.0
33.2
33.4
33.6
33.8
34.0
34.2
34.4
NORTH PACIFIC OCEAN
SURFACE SALINITY (‰)
SUMMER 1958
30.5
31.0
31.5
32.0
32.2
32.4
32.6
32.8
33.0
33.2
33.4
33.6
33.8
34.0
34.2
34.4
34.6
34.8

FIG. 10. Surface salinity, summer 1957 and summer 1958.

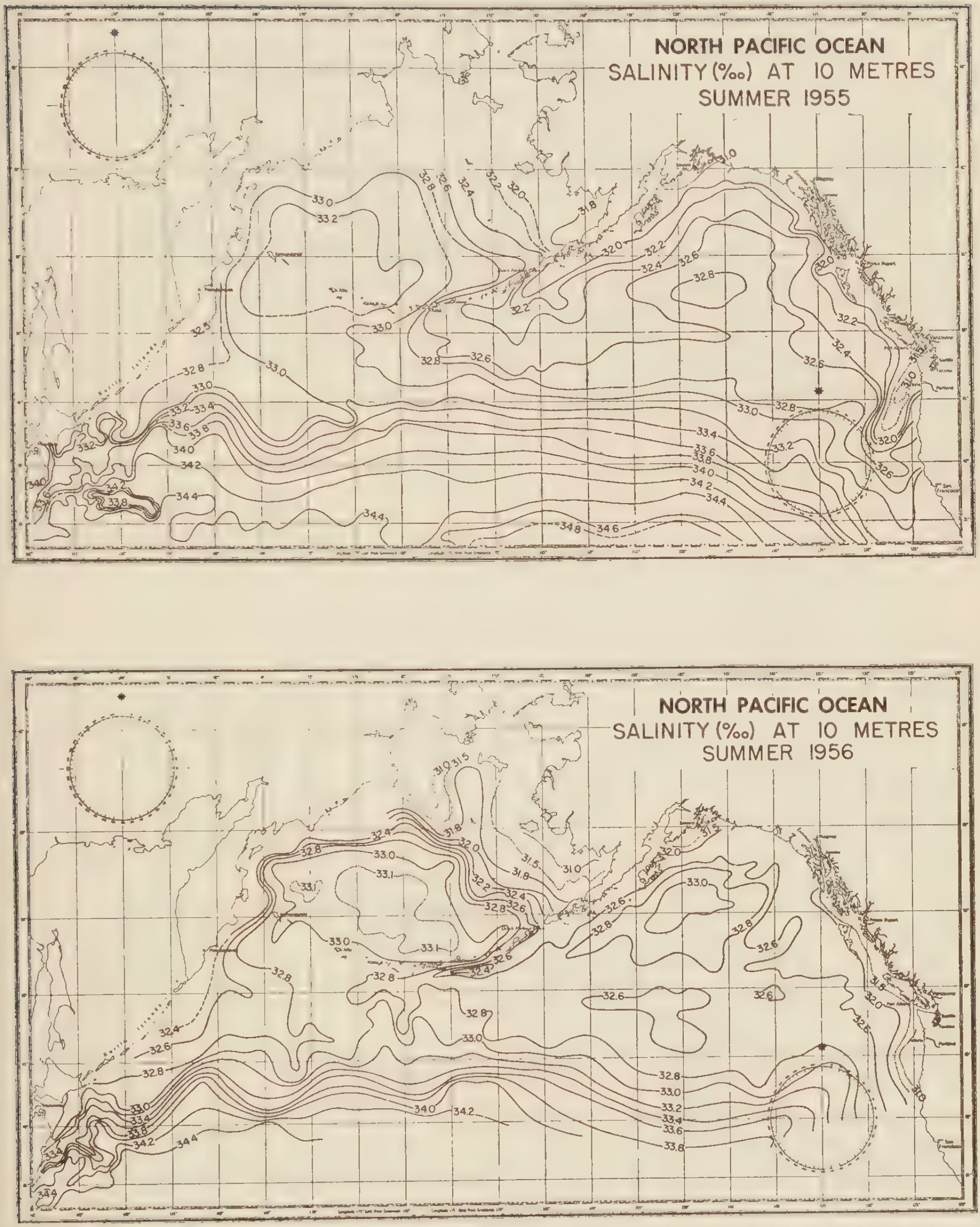

NORTH PACIFIC OCEAN
SALINITY (‰) AT 10 METRES
SUMMER 1955
NORTH PACIFIC OCEAN
SALINITY (‰) AT 10 METRES
SUMMER 1956

FIG. 11. Salinity at 10 metres, summer 1955 and summer 1956.

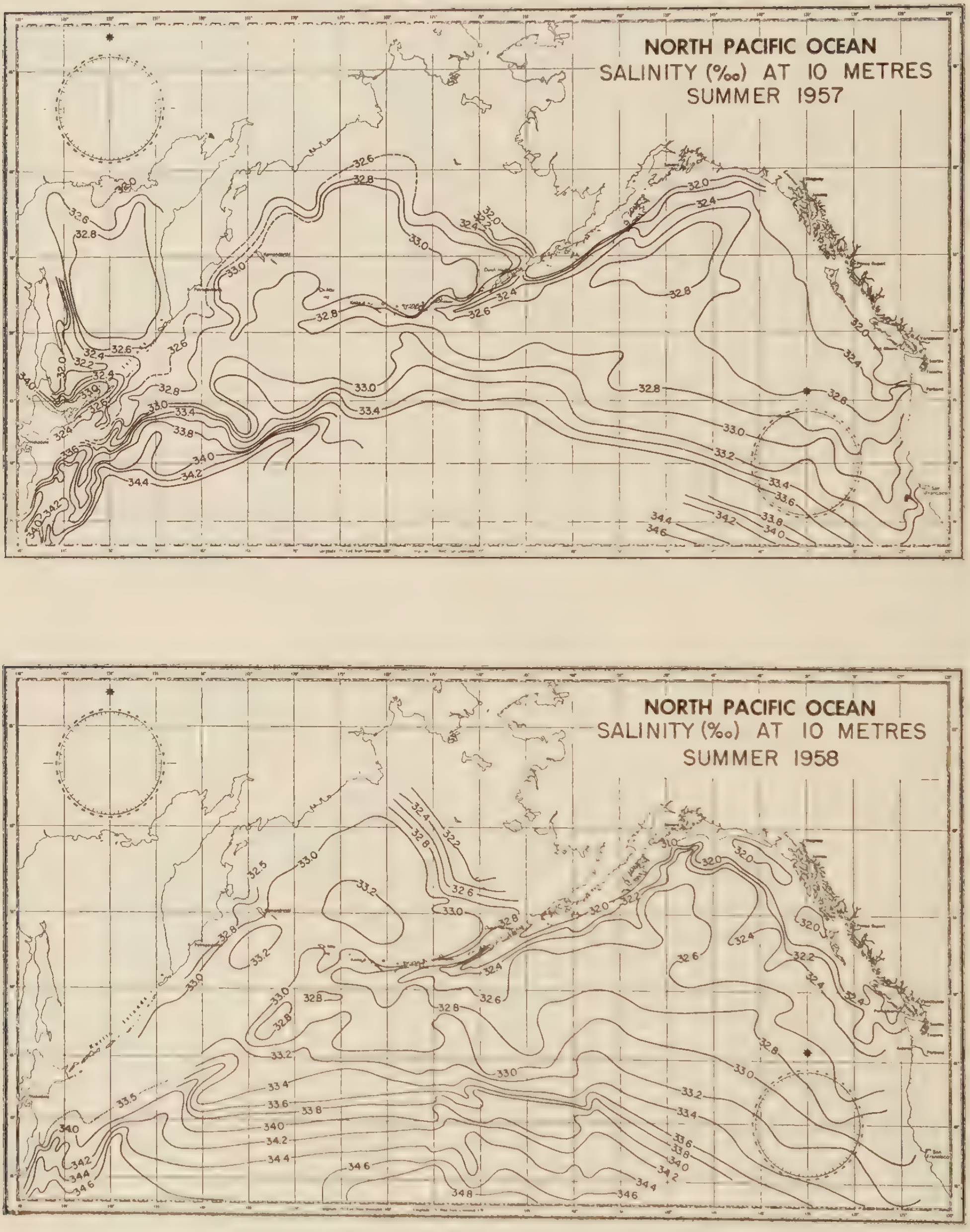

NORTH PACIFIC OCEAN
SALINITY (‰) AT 10 METRES
SUMMER 1957
32.0
32.2
32.4
32.6
32.8
33.0
33.2
33.4
33.6
33.8
34.0
34.2
34.4
34.6
NORTH PACIFIC OCEAN
SALINITY (‰) AT 10 METRES
SUMMER 1958
32.0
32.2
32.4
32.5
32.6
32.8
33.0
33.2
33.4
33.5
33.6
33.8
34.0
34.2
34.4
34.6
34.8

FIG. 12. Salinity at 10 metres, summer 1957 and summer 1958.

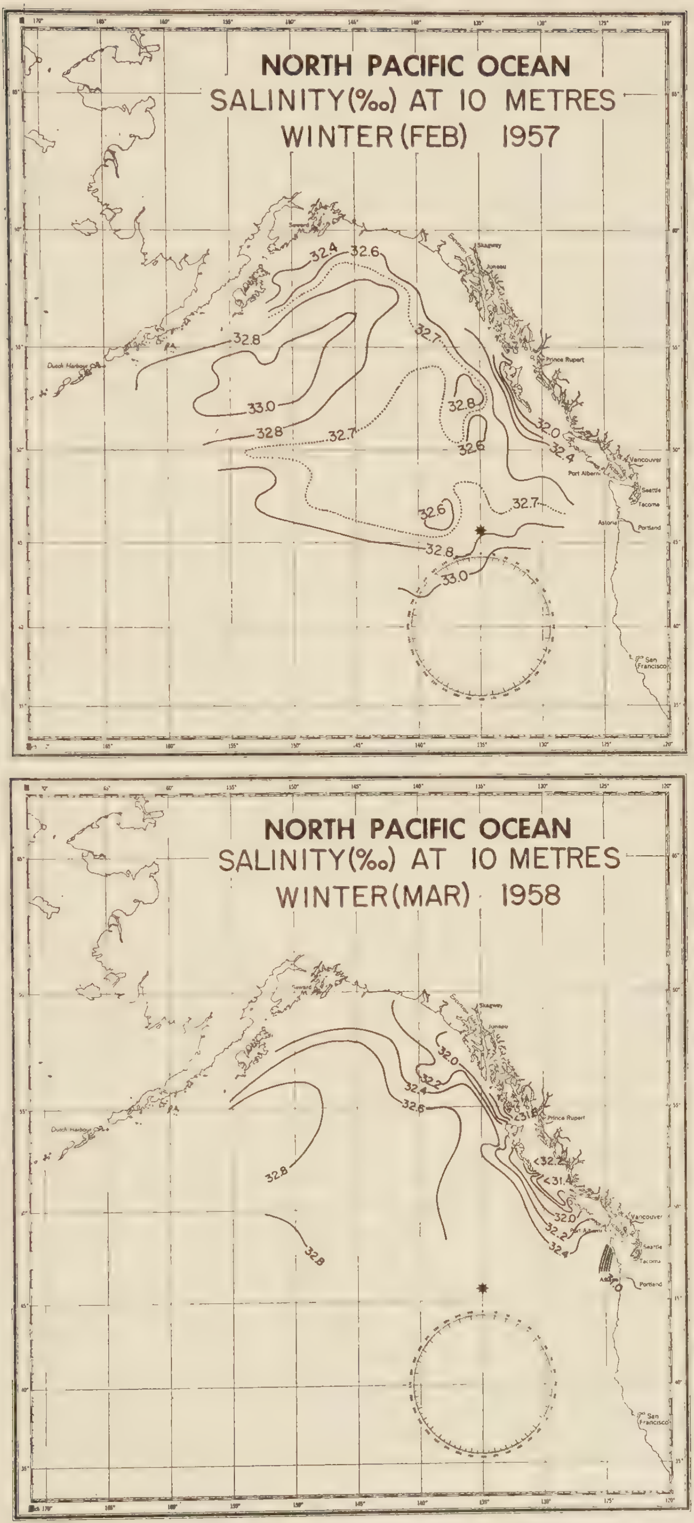

NORTH PACIFIC OCEAN
SALINITY(‰) AT 10 METRES
WINTER (FEB) 1957
32.4
32.6
32.7
32.8
33.0
32.0
32.4
32.6
32.7
32.8
33.0
Seward
Skagway
Juneau
Prince Rupert
Dutch Harbour
Port Alberni
Vancouver
Seattle
Tacoma
Astoria
Portland
San Francisco
NORTH PACIFIC OCEAN
SALINITY(‰) AT 10 METRES
WINTER(MAR) 1958
32.0
32.2
32.4
32.6
<31.8
<32.2
<31.4
32.0
32.2
32.4
32.8
32.8

FIG. 13. Salinity at 10 metres, winter (Feb) 1957 and winter (March) 1958.

Sea and the central Okhotsk Sea during the summer. These, too, are believed to be permanent features. The surface salinity in the maxima is about 33‰. Along the entire coastline bounding the region (with the exception of the American coast south of Vancouver Island) the surface salinities in general decrease to values less than 32‰. This is due to land drainage and/or to fresh water released by the melting of sea ice, and is more pronounced in summer than in winter. The summer values are especially low in areas such as Bristol Bay in Alaska, and the Gulf of Anadyr in Siberia, primarily because of ice melt. A localized minimum, often present off the Columbia River (Fig. 9), is presumably due to discharge from that river. The trend toward increased surface-layer salinities off the California coast in summer result both from the lack of land drainage, and from the tendency to upwelling associated with the northwesterly winds prevalent in the locality during this period (Fig. 3).

Southward of the permanent maximum in the Gulf of Alaska, the salinity decreases to about 32.6‰ in the vicinity of Lat. 50° N and then increases through the Polar Front. This sequence represents another permanent feature. A fairly marked gradient characterizes the Polar Front Region, values increasing as much as 0.8‰ meridionally across the Front. Off the northern Japanese islands the distribution exhibits at all times marked irregularities which occur in the area of confluence of the low-salinity Oyashio and the high-salinity Kuroshio.

In the eastern portion of the Subarctic, the only part of the region for which significant winter data are available, the surface salinities appear to be slightly greater in the winter than in the summer. This winter increase is attributable to two main causes; the greater extent of mixing between surface and deep water due to storms and convectional effects, and the lessened supply (due to snow and ice storage) of fresh water from land drainage (Dodimead, 1958).

3. Vertical Sections of Salinity

Representative salinity structures may be drawn from the data observed along the Sections shown in Fig. 14. These Sections, shown in Fig. 15 through 19 vary from 250–1000 m in depth. In the western Pacific and Aleutian regions (Sections 1 through 7, Fig. 15 and 16) observations were made only in the summer. In the eastern Pacific (Sections 8, 9 and 10, Fig. 17, 18 and 19) both summer and winter data are available.

The sections reveal the presence, in the Subarctic Region, of the principal halocline between about 100 and 200 m depth, and show that the bottom of the halocline, when it exists, can be quite faithfully delineated by the position of the 33.8‰ isopleth (Tully and Dodimead, 1957). Below this, the gradual increase of salinity with depth is also shown. In addition, Sections 1 and 8 reveal the degradation of the halocline with decreasing latitude as was shown in Fig. 8 and discussed on page 132. In the Polar Front, the water at intermediate depths (200–500 m) becomes effectively isohaline (although slight inversions may occur); a salinity minimum develops below 300 m depth at the southern limit. In the Subtropic Region a negative gradient of salinity exists in the upper layers, and no halocline is present.

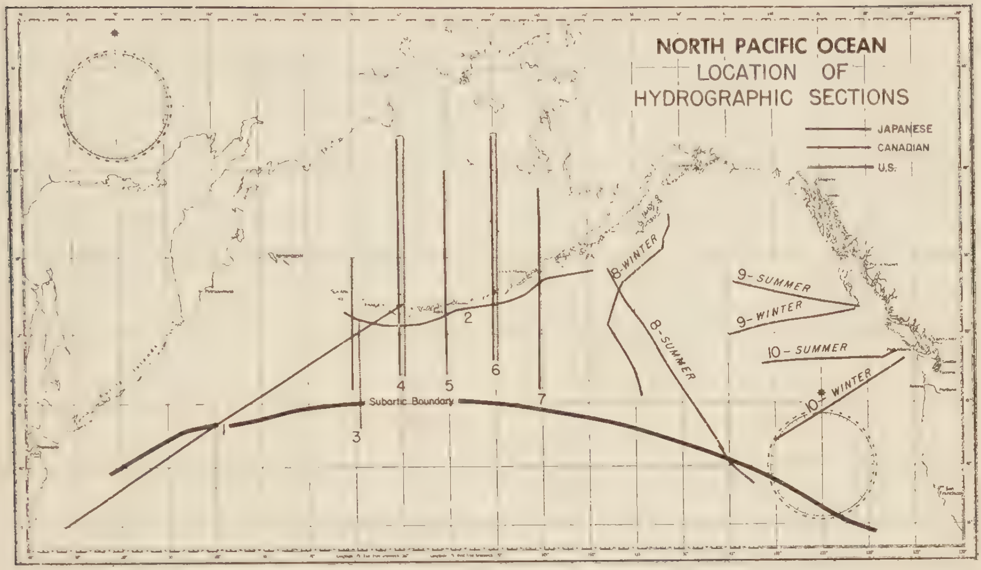


FIG. 14. Location of Hydrographic Sections.

A feature of the effectively north-south Section 8 (Fig. 17) in the eastern part of the region is the "dome-like" configuration exhibited by the deeper isohalines. This anticline structure is a permanent feature and is presumably associated with the dynamics of the anti-clockwise circulation of the Alaska Gyre (Bennett, 1959). The halocline, however, is continuous throughout the area of the dome. An upper-zone salinity maximum occurs in this area. Its existence leads to important conclusions regarding the means of replenishment of saline water in the upper zone (page 169).

Sections 3 through 7 across the Aleutian Island Chain reveal the three-zone structure typically present south of the islands, and the deepening of the halocline by the mixing occurring in the island passages. Strong gradient currents and intensive mixing at the edge of the continental shelf in the Bering Sea (page 120) are revealed by the marked inclination of the isohalines at the northern extremity of these sections. Also a deep-zone dome structure was present in 1956 south of the Aleutian Islands. It is unknown at this time whether it too is a permanent feature.

F. TEMPERATURE OF SUBARCTIC WATERS

Amounts of heat, giving rise to variations of surface temperature significant on even a diurnal scale, are gained from, or lost to, the surroundings by the oceans (Tabata, 1960). Effectively all the heat supplied to the oceans comes originally from the sun. Over 85% of the sun's radiation penetrating the sea surface is absorbed within the first 10 m of clear oceanic water. In turn, heat is dissipated from the oceans, mainly by evaporation, back radiation, and conduction of sensible heat to the atmosphere. These processes are modified in turn by

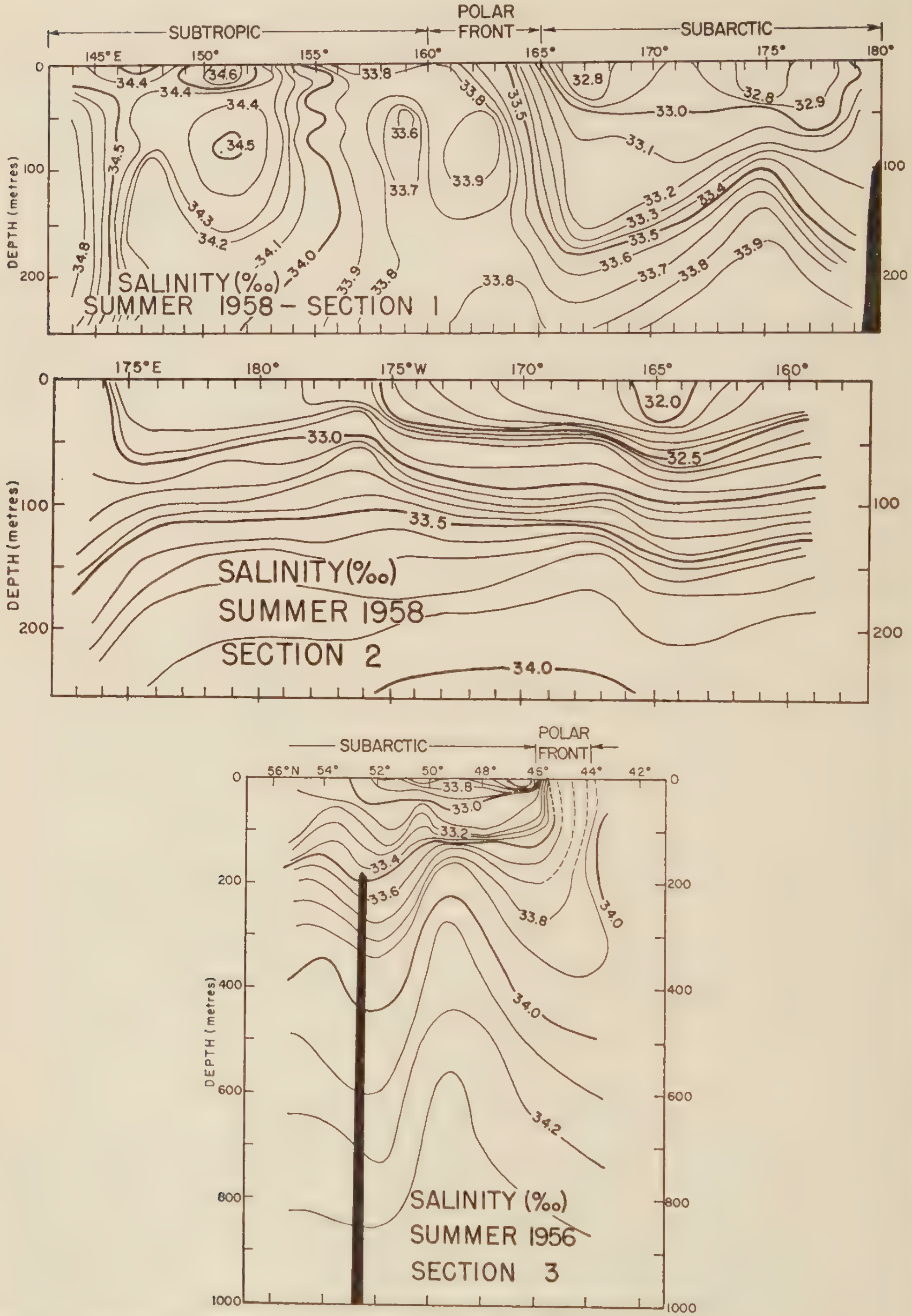


FIG. 15. Salinity, Section 1, summer 1958, Section 2, summer 1958 and Section 3, summer 1956.

such factors as wind and cloud cover. Obviously sea temperatures will increase when heat gain exceeds heat loss and will decrease when loss exceeds gain.

Two heating cycles occur in the sea: a diurnal and a seasonal. In the former, surface waters are heated during the day and cooled during the night. This process occurs throughout the entire year. However, a lag of several hours exists between this cycle (as represented by the change in sea-surface temperature) and that of the sun's position. The maximum temperature occurs in the late afternoon rather than at noon.

In the Tropic Region, the diurnal cycle is such that the daytime heat gain equals nighttime loss. As a result the mean daily sea-surface temperature remains constant throughout the year (at about 25 to 28° C). However, at higher latitudes, there exists a daily net heat gain during the heating period,

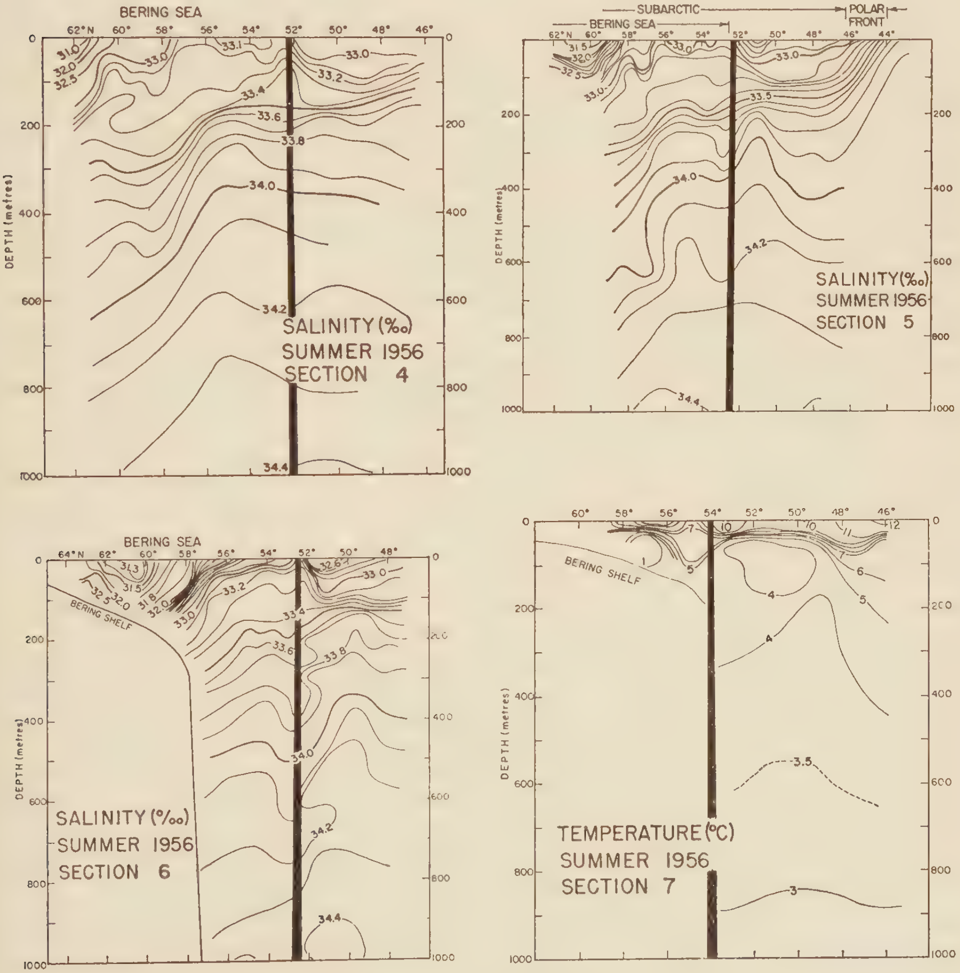


FIG. 16. Salinity, summer 1956, Sections 4, 5, 6 and 7.

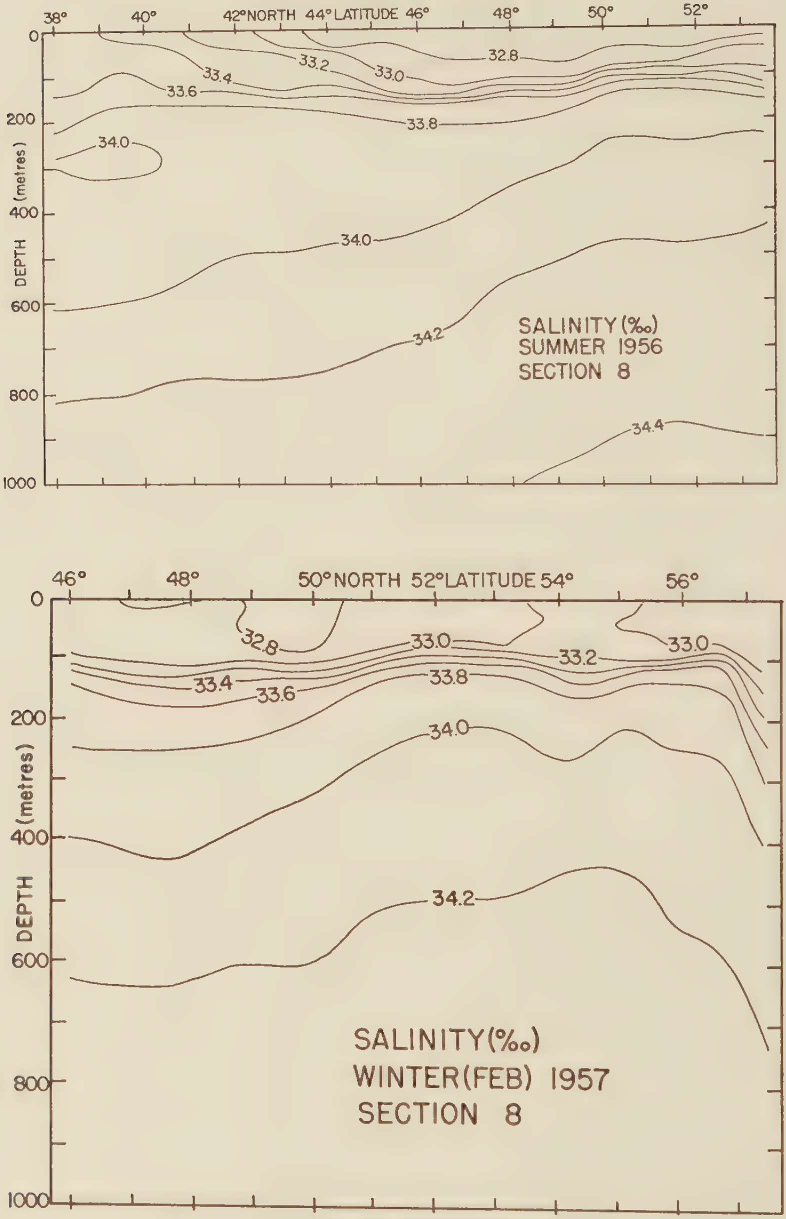


FIG. 17. Salinity, Section 8, summer 1956 and winter (Feb) 1957.

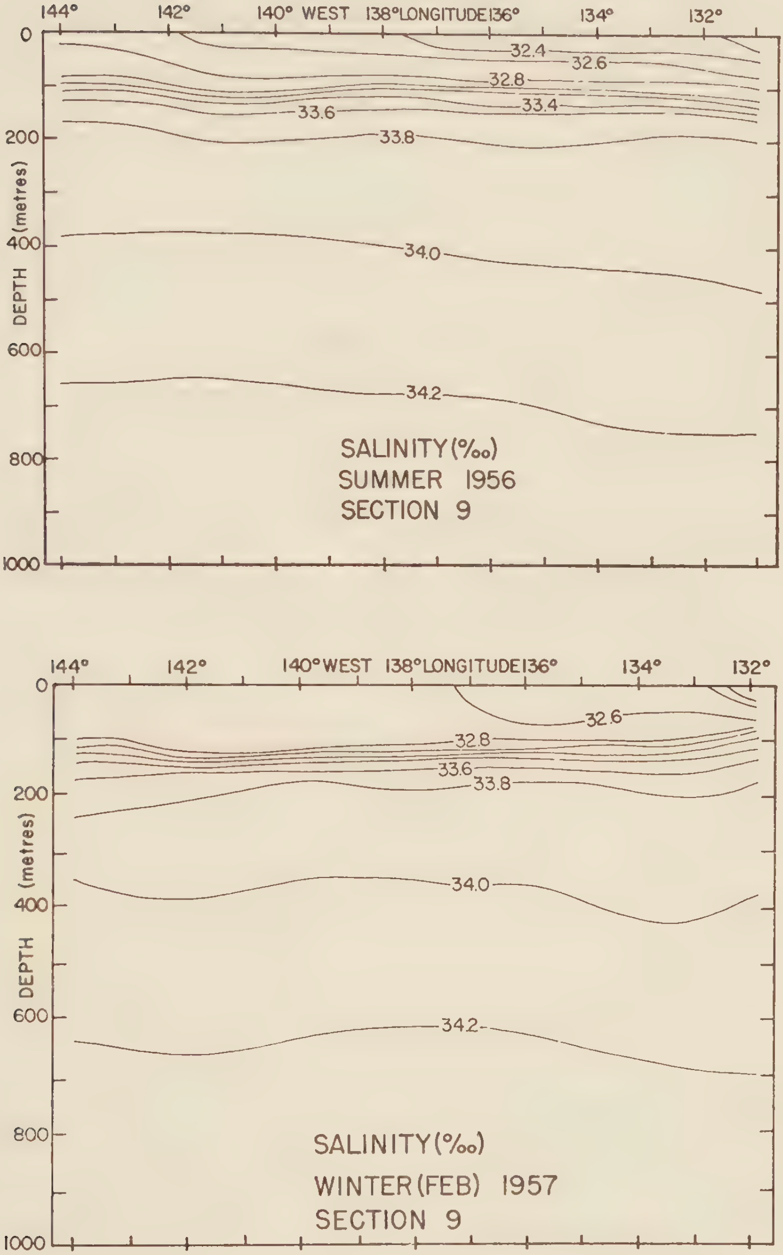


FIG. 18. Salinity, Section 9, summer 1956 and winter (Feb) 1957.

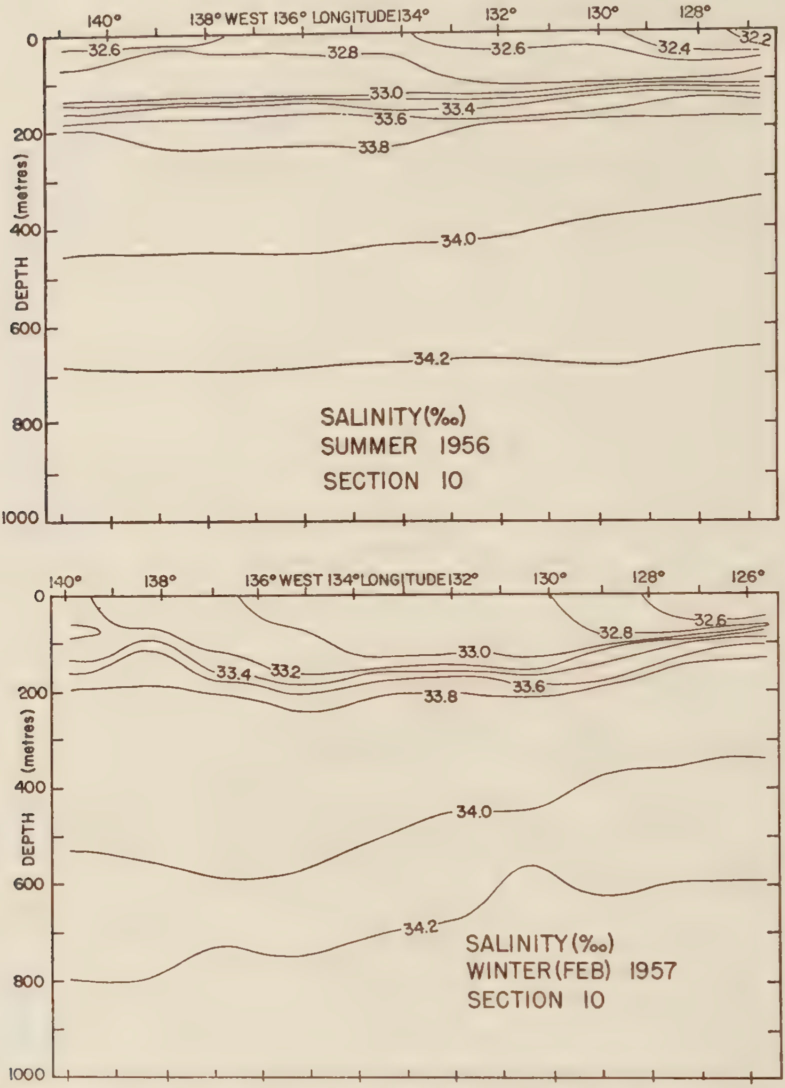


FIG. 19. Salinity, Section 10, summer 1956 and winter (Feb) 1957.

i.e. during the middle six months of the year, while a daily net heat loss occurs during the cooling period—the remaining months. This seasonal effect, compounded of the individual diurnal effects, becomes more pronounced with increasing latitude. In the Subarctic Region, the heat gain and heat loss are effectively in balance at the equinoxes, at the end of March and at the end of September. Fig. 20 shows, for the Subarctic, both a typical annual (seasonal) cycle of the net heat transfer across the sea–atmosphere interface and the accompanying sea-surface temperature cycle. The data were obtained at Ocean Weather Station "P" (Lat. 50° N, Long. 145° W) (Fig. 1). It is seen that, in the open ocean, the times of maximum and minimum sea-surface temperature coincide with the two times of no net heat transfer. Any marked deviations from this conditions would presumably be due to effects upon the surface waters by horizontal and/or vertical eddy or advective processes (Tabata, 1960).

In the western Pacific, particularly in the region of confluence of Kuroshio and Oyashio (Fig. 7), advection of heat in the fast flowing currents is a considerable factor. Watanabe (1955) has shown that the magnitude of heat transport was frequently of the same order as the heat exchange at the surface. Koizumi (1956) proved that, on an annual average, the amount of heat brought into the region of Ocean Station "X" (Lat. 39° N, Long. 153° E) (Fig. 1) is comparable to the amount of heat lost there by evaporation, or to about twice the amount lost by back radiation.

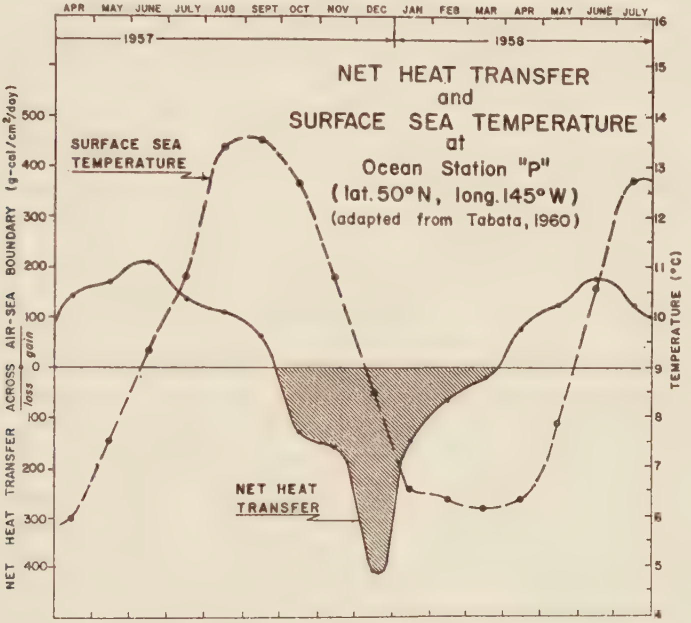


FIG. 20. Annual cycle of net heat transfer and of sea-surface temperature at Ocean Station "P" (adapted from Tabata, 1960).

1. TEMPERATURE STRUCTURE

During the heating period, the heat is accumulated and is gradually mixed downward. A single structure of temperature predominates in the Subarctic at this time (Fig. 21). There is a shallow isothermal surface layer which corresponds to the surface isohaline layer (page 131). It results, similarly, from mixing by the light winds prevailing during the period. Below the surface layer, a sharp negative thermocline is present. Below this, there follow in turn another shallow isothermal layer and, over much of the area, a positive thermocline. The latter extends to a depth of about 150 m. This temperature inversion is

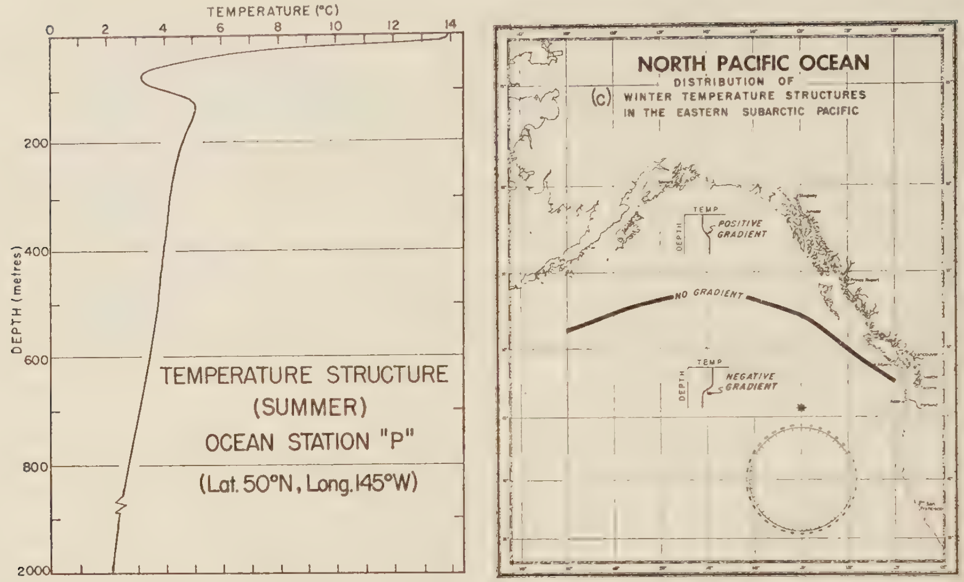


FIG. 21. Temperature structure at Ocean Station "P", summer and distribution of winter temperature structures in the Eastern Subarctic Pacific (after Dodimead, 1958).

density-stable, since it occurs within the principal halocline. Below this, the temperature decreases regularly with depth to about 2° C at 2000 m.

The upper isothermal layer slowly warms and deepens (to a maximum depth of about 30 m) until the end of the heating period, about the end of September. After this time, the surface waters are cooled, and are mixed downward both by convection and by the strong winds of autumn and winter. These conditions lead to the formation of the *two* distinct temperature structures which occur widely throughout the region in winter (Fig. 21). In both cases, the upper layers become isothermal (and isohaline) from the surface to a depth of about 100 m. By late winter the zone has attained its minimum temperature of the year. The structure (a) is typical of that occurring in the northern part of the region. The profile indicates that a positive gradient (thermocline) exists below the isothermal layer. The warmer water at this depth is density-stable because the thermocline occurs within the principal halocline. In this case, the cooling (net heat loss) is great enough so that the upper 100 m of water become colder than the deeper water. By contrast, the structure in the southern part of the region is still characterized by a negative thermocline. This, however, is much less pronounced than the summer thermocline. Here the surface cooling is insufficient to render the surface layers colder than those at depth. The distribution of these two structures throughout the eastern Subarctic is shown in the latter diagram of Fig. 21. Northward and southward of the boundary between the two types of structure, the positive and negative thermoclines become more pronounced. Isothermal conditions, arising as a result of convective overturn, prevail in winter from surface to bottom in the shallow portions of the Bering Sea. These conditions are caused by the removal of fresh water in ice formation, rather than by convection induced by surface cooling.

In the Polar Front Region, the upper zone is often characterized by one or more temperature inversions. These are possible because of the existence of associated haloclines (page 132). In the Subtropic Region an isothermal upper zone, averaging about 20 m in depth, is maintained permanently by the prevailing Westerlies. Below this zone there is a negative thermocline, also permanent, which extends to a depth of 500–600 m.

In all three regions, the temperature structure in the deeper waters (below the winter depth of the thermocline) is not influenced to any significant degree by heating and cooling effects originating at the surface. It may, however, vary because of advectional effects (see for example, page 148).

(i) DICHOTHERMAL AND MESOTHERMAL TEMPERATURE STRUCTURES. In the western and central Subarctic Region, during the summer, there is usually a temperature minimum at about 100 m depth. The structure which is associated with this minimum, and which is apparently peculiar to the Subarctic Region, is termed *dichothermal* (Uda, 1935, 1955, 1958). Fig. 22 and 23 illustrate the horizontal distribution of the dichothermal (minimum) temperature in the Subarctic Region, during the summers of 1955 through 1958.

Bennett (1959) has shown that dichothermal structure is not continuous throughout the eastern Subarctic Region. Instances where the structure does *not* occur have *not* been shown in the figures.

The dichothermal structure can be classified into three types, according to the mode of formation and subsequent behaviour. One type is a consequence of the seasonal cycle of heating and cooling. It occurs in those areas where, during the winter, the waters in the upper zone become colder than the waters in the halocline (e.g. Gulf of Alaska, Fig. 21, Sea of Okhotsk, Bering Sea, etc.). A *positive* gradient (thermocline) is formed in the halocline below an isothermal upper zone. With the advent of the summer period, the temperature of the surface layers increases and an overlying negative thermoline is formed. As the period progresses and the heating continues, this thermocline grows and deepens. In this type of dichothermal structure there is an isothermal "temperature-minimum" layer situated between the upper negative and the lower positive thermocline. The layer generally occurs just above the halocline (60–100 m depth). The characteristic temperature ($T_{minimum}$) changes very little during the course of the summer period (Dodimead, 1961). During the following period of net cooling the upper thermocline is progressively erased; the dichothermal structure vanishes and is replaced by the winter structure typical of the area.

A second type of dichothermal structure originates, by the same process, in the areas of sea-ice production, chiefly the Okhotsk Sea. The cold, more saline iso-layer remaining after the formation of the ice extends to depths which are generally within the shallow and narrow halocline present in this sea. The temperature of this layer is between –1.8 and –1° C. The layer (in the Okhotsk

Sea) follows the persistent circulation (page 129) and moves through the middle Kurile passages into the western Pacific. Because of mixing along its path, especially in the island passages, the layer becomes warmer (to about 1° C). A portion of the layer underruns the upper layers of the warm (to 20° C) saline (to 35‰) Kuroshio to form the greatest part of the Oyashio Undercurrent. The resulting temperature minimum at depth represents the second type of

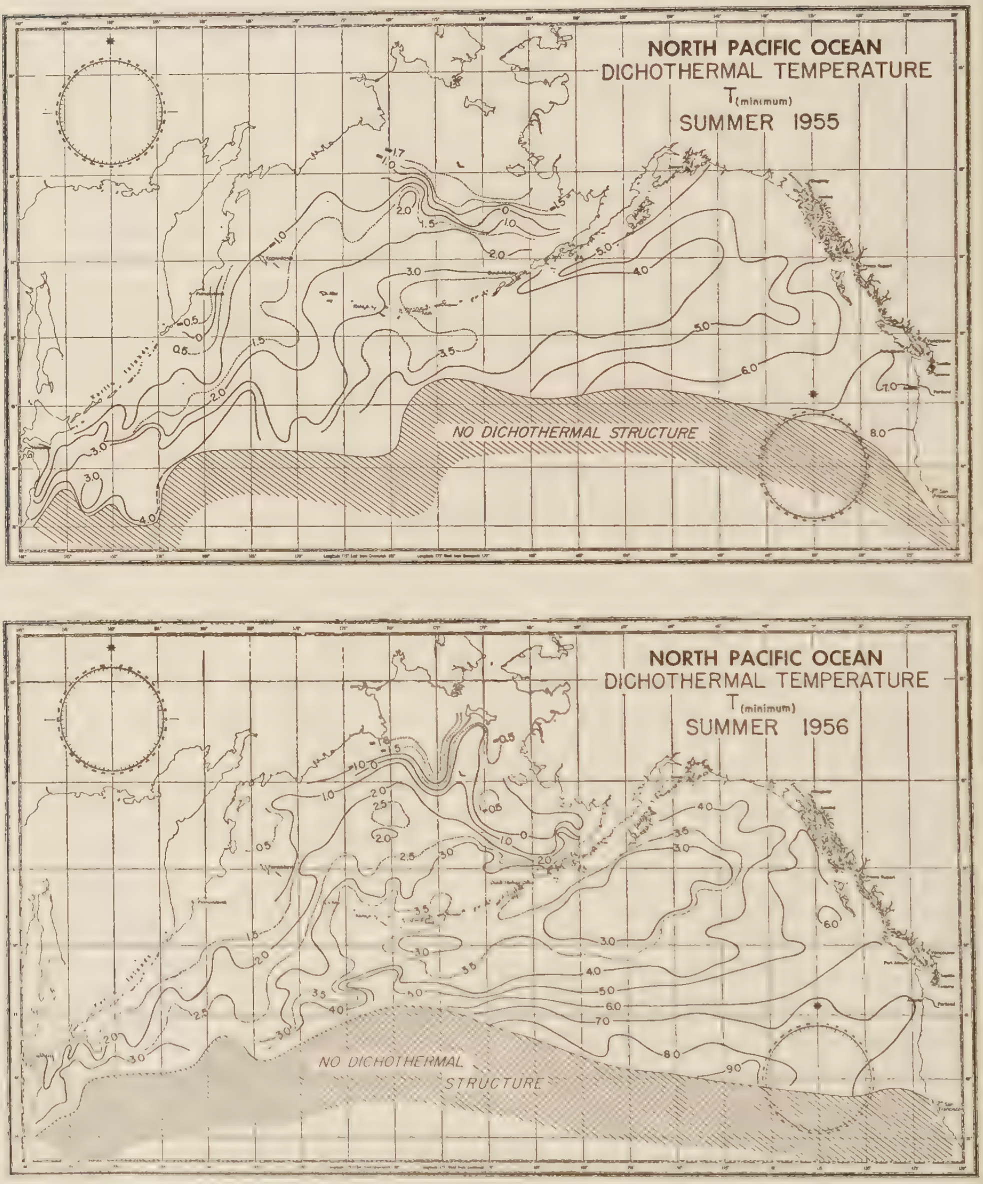

NORTH PACIFIC OCEAN
DICHOTHERMAL TEMPERATURE
$T_{(minimum)}$
SUMMER 1955
NO DICHOTHERMAL STRUCTURE
-1.7
-1.0
-1.5
0
0.5
1.0
1.5
2.0
3.0
3.5
4.0
5.0
6.0
7.0
8.0
NORTH PACIFIC OCEAN
DICHOTHERMAL TEMPERATURE
$T_{(minimum)}$
SUMMER 1956
NO DICHOTHERMAL
STRUCTURE
-1.5
-1.0
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
5.0
6.0
7.0
8.0
9.0

FIG. 22. Dichothermal temperature, summer 1955 and summer 1956.

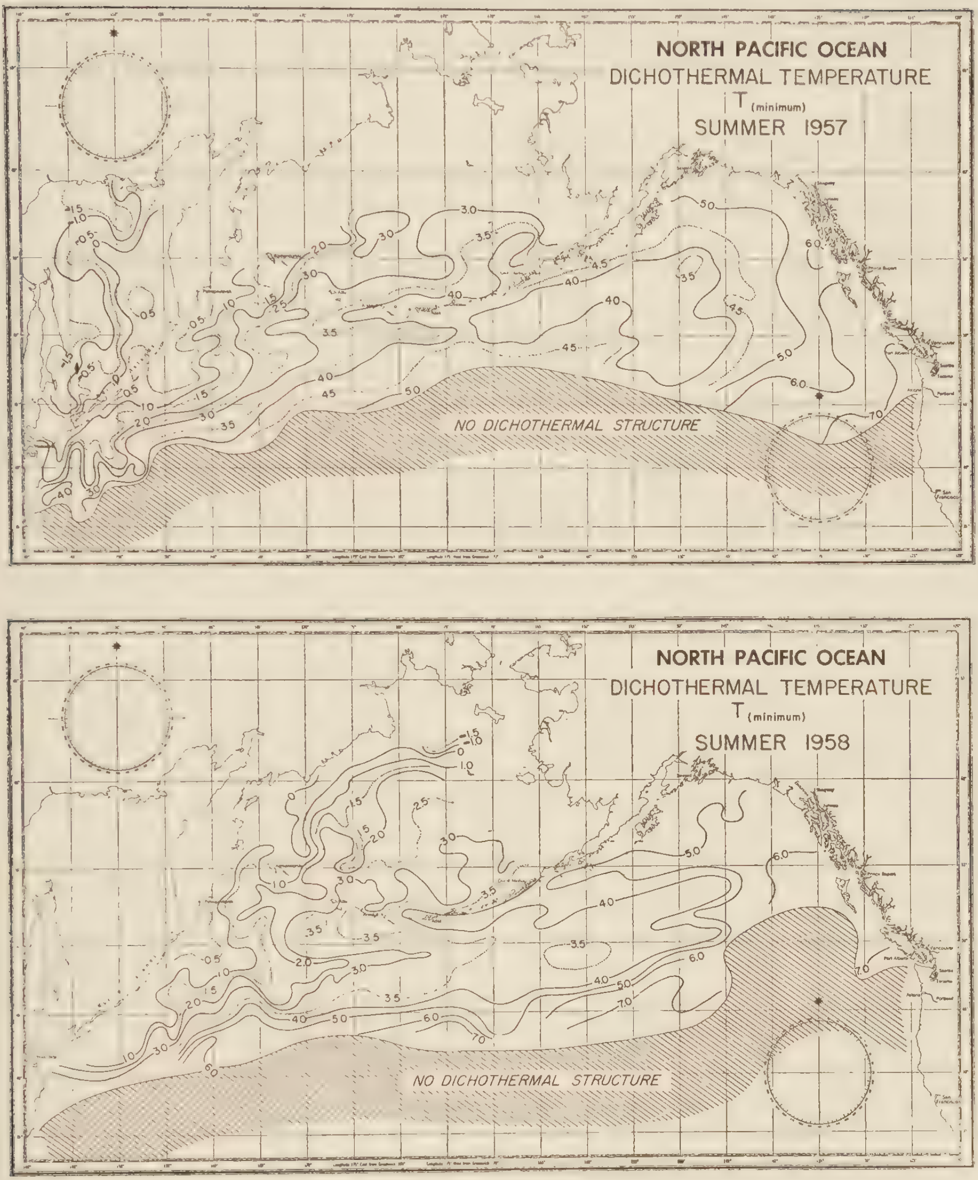

NORTH PACIFIC OCEAN
DICHOTHERMAL TEMPERATURE
T (minimum)
SUMMER 1957
NO DICHOTHERMAL STRUCTURE
NORTH PACIFIC OCEAN
DICHOTHERMAL TEMPERATURE
T (minimum)
SUMMER 1958
NO DICHOTHERMAL STRUCTURE

FIG. 23. Dichothermal temperature, summer 1957 and summer 1958.

dichothermal structure. The passage at depth of the water through the Kurile passages and its (modified) continuation as the Undercurrent can be "traced" by the horizontal distribution of dichothermal temperature as shown, for example, in Fig. 22. It may be noted that the progress of the Undercurrent (which is relatively fresh compared to Kuroshio water) can also be followed by means of a salinity minimum at depth. The outflow through the middle Kurile passes (and thus the second type of dichothermal structure) persists throughout the *entire year.* The strength of the Undercurrent varies from year to year and appears to be intimately related to the meteorological conditions in the area (page 173).

Another and third type of structure results from the presence of warm water under a colder and therefore, of necessity, a less saline layer. This type is believed to originate when warm saline Polar Front (or Subtropic) water in the sub-surface layer, intrudes into the Subarctic Region. The intruding water is cooled and sinks, but remains warm enough to form a temperature maximum at depth. The water associated with this temperature *maximum* is termed *mesothermal water.* The depth of its upper boundary appears generally to be limited by the presence of the principal halocline. *Below* the halocline, a considerable depth (to several hundred metres) of effectively isothermal warm water can persist. The dissolved oxygen content of this water should be small because of the screening from surface aeration (due to the great stability inherent in the halocline). An example of mesothermal structure is observed between about 170° W and 180° longitude extending from south of the Aleutian Islands into the Bering Sea. It results in great part from the northward intrusion, at depth, of the (seasonal) South Aleutian Warm Current (page 171). In this case, the water appears to subside along the isopycnal (isentropic) surface having $\sigma_t = 27.20$. This value corresponds, in this area, to temperature about 3.6°C and salinity 34.1‰ (e.g. Fig. 16).

In the absence of intervening advectional effects, both the value and the depth of the (summer) dichothermal temperature provide information on the conditions prevailing during the preceding winter (Dodimead, 1961). These quantities indicate very closely the temperature and depth of the homogeneous upper layer (regardless of whether that layer was formed primarily by wind mixing or by convective overturn induced by sea-ice formation).

Figures 22 and 23 illustrate that dichothermal structure is, in summer, present in some form throughout most of the Subarctic Region. It is seen that the southern limit of the structure corresponds closely to the southern boundary of the region, as defined by the salinity structure. There appears to have been a marked southward extension of dichothermal structure since 1940 (Uda, 1955).

2. Horizontal Distribution of Temperature

The distributions of temperature in the near-surface (10 m) waters are shown in Fig. 24, 25 and 26. They correspond to the salinity data shown in Fig. 11, 12 and 13.

During the summer the general configuration of the isotherms is east–west, except near the continental margins. The winter data are sparse and limited to the Gulf of Alaska. However, they indicate that the pattern is similar to that of summer, although the water is about 7 C° colder. This is confirmed by the monthly mean sea-surface temperature charts published by the U.S. Weather Bureau (1938).

Figures 24, 25 and 26 show the Polar Front as a meridional gradient of temperature from about latitude 35° to 45° N, somewhat broader than the Front defined by salinity (page 132).

Northward of this Front, in the Gulf of Alaska, there is an area of temperature minimum. This cold centre is commonly regarded as the dynamic centre of the Alaska Gyre (Fig. 7). In summer it appears to coincide with the centre defined by the salinity maximum (page 139) but in winter the two appear to be separated.

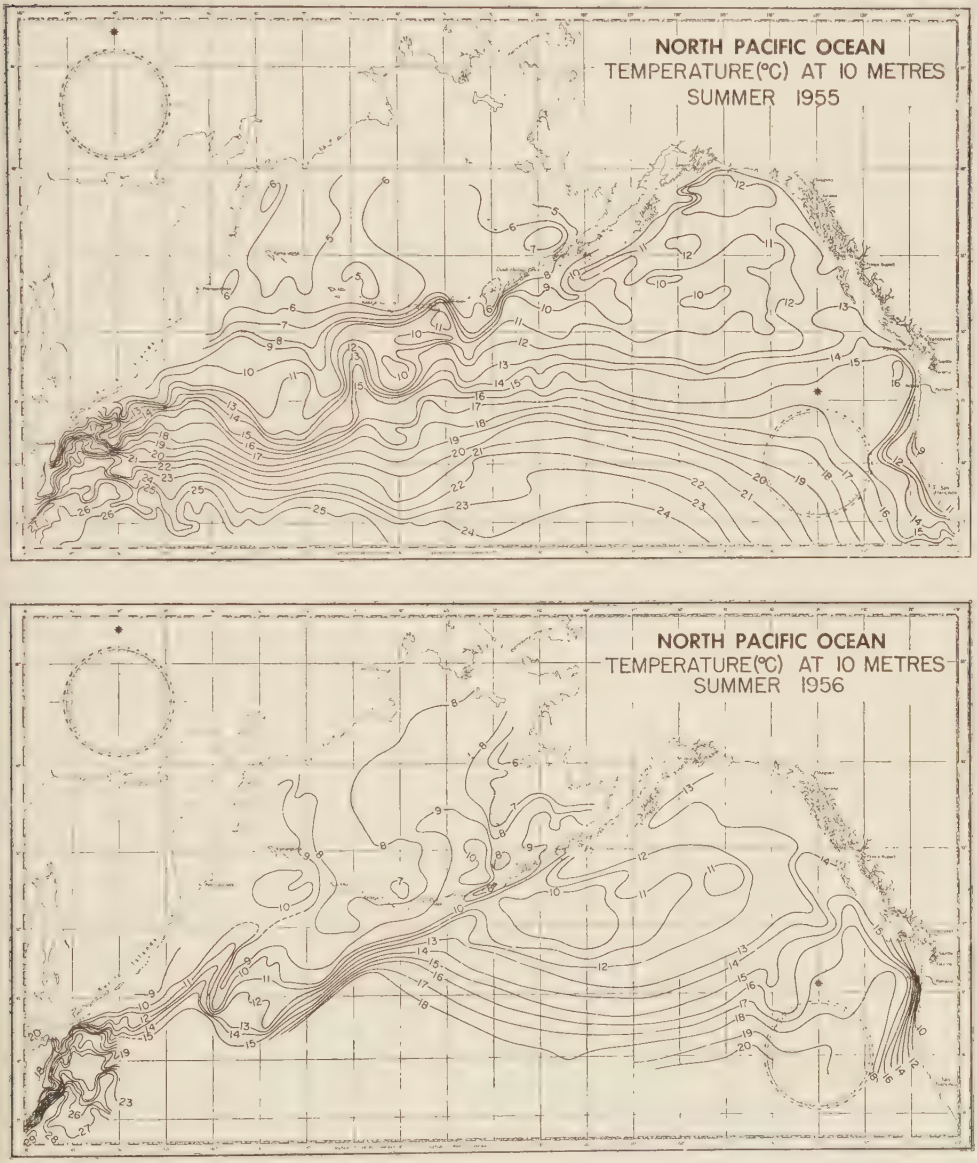

NORTH PACIFIC OCEAN
TEMPERATURE(°C) AT 10 METRES
SUMMER 1955
NORTH PACIFIC OCEAN
TEMPERATURE(°C) AT 10 METRES
SUMMER 1956

FIG. 24. Temperature at 10 metres, summer 1955 and summer 1956.

Off the northern Japanese islands there are several "filaments" of closely-spaced isotherms. These indicate the distinct fronts associated with the confluence of the warm Kuroshio and cold northern waters (page 127). Actually, the conditions there are much more confused than shown, because of the turbulent nature of the currents and the short term variability in the boundaries between the water masses (Uda, 1938a, b).

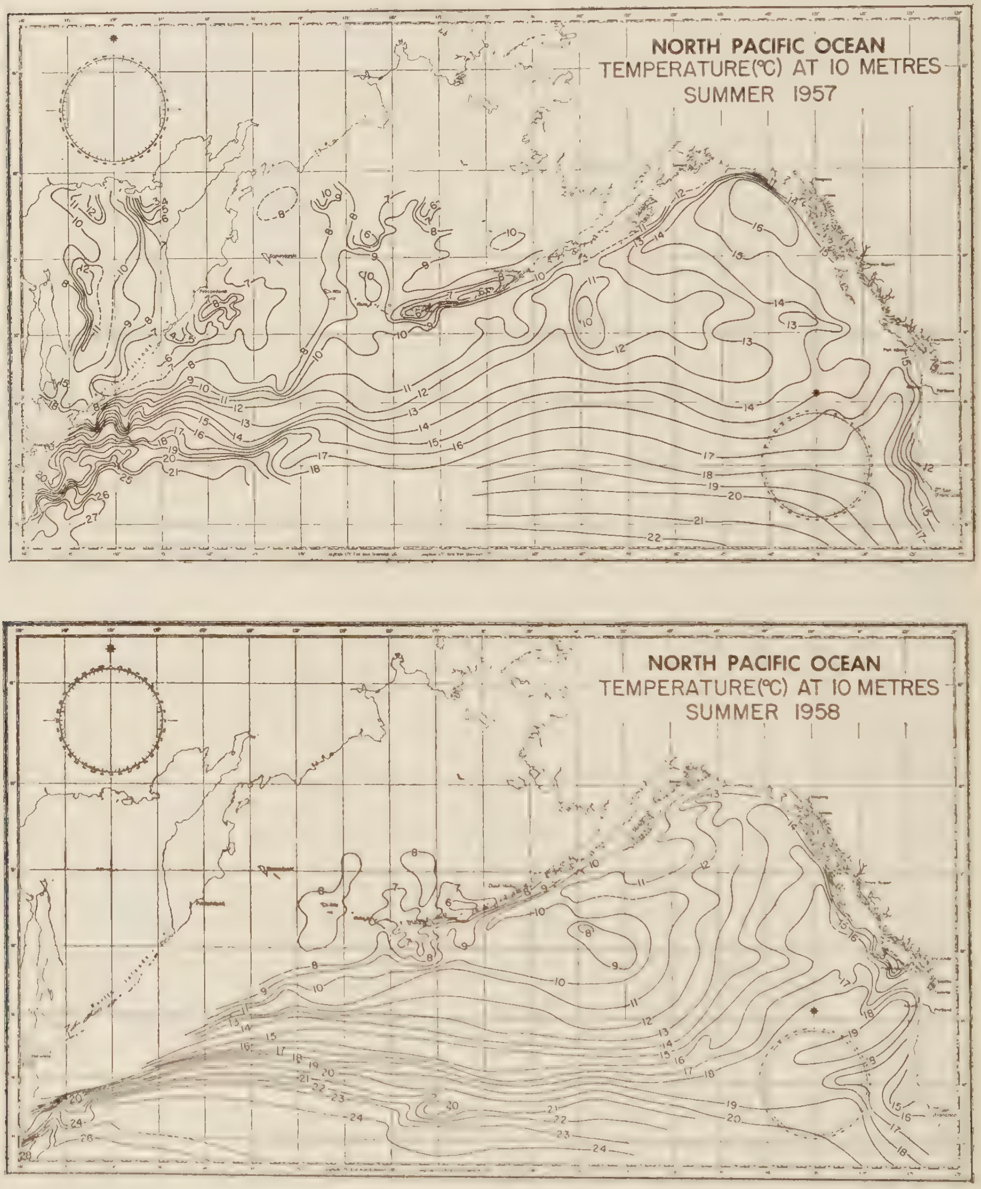

NORTH PACIFIC OCEAN
TEMPERATURE(°C) AT 10 METRES
SUMMER 1957
NORTH PACIFIC OCEAN
TEMPERATURE(°C) AT 10 METRES
SUMMER 1958

FIG. 25. Temperature at 10 metres, summer 1957 and summer 1958.

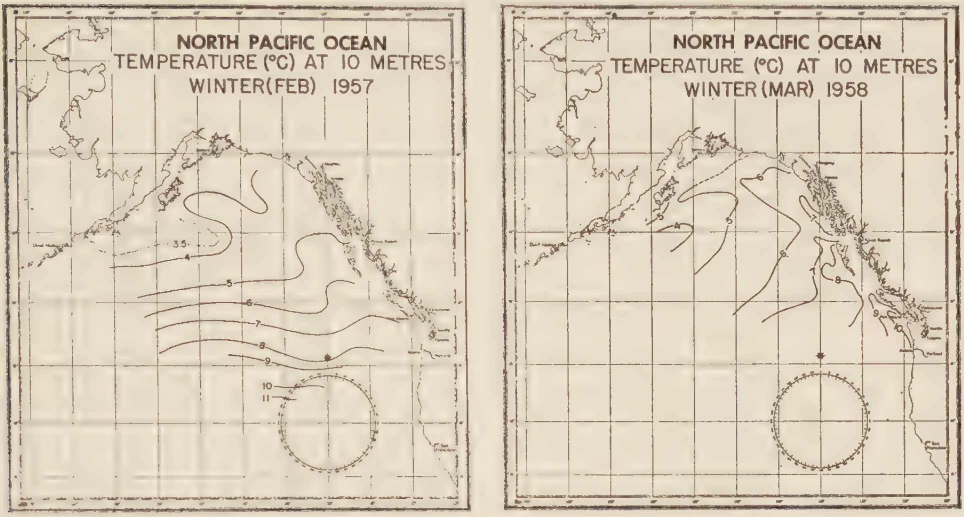


FIG. 26. Temperature at 10 metres, winter (Feb) 1957 and winter (March) 1958.

3. VERTICAL SECTIONS OF TEMPERATURE

Vertical sections of temperature, corresponding to those previously given for salinity (Fig. 15 through 19) are shown in Fig. 27 through 31. The sections representing summer conditions in the open ocean (e.g. Lines 8, 9 and 10) clearly show the marked seasonal thermocline in the upper few tens of metres.

The upper zone temperature is a function of latitude in both winter and summer. A detailed examination shows, however, that the seasonal *range* of temperature is about 7 C° and is effectively constant with latitude throughout the Subarctic and most of the Polar Front. In the Subtropic Region, the annual range of temperature decreases with latitude.

A dome-like structure, similar to that found for salinity (page 139), characterizes the deep zone in the vicinity of the Alaska Gyre. The thermocline exists and is continuous throughout the area of the Gyre. The summer sections through the Aleutian Islands show the disappearance of the summer thermocline because of the mixing occurring in the island passages. A dome-like structure is indicated in the deeper water, south of the Aleutians, as in the case of salinity.

G. DENSITY STRUCTURE

The density of sea water is a function both of its temperature and salinity. Generally, in the Subarctic Pacific, the density structure is dominated by the salinity.

Density (σ_t) structure typical of winter and of summer is depicted in Fig. 32. σ_t is defined by: (specific gravity -1×1000). Subarctic winter and summer structures differ markedly. In winter, effectively isopycnal (isothermal and isohaline) conditions occur throughout the upper zone. In summer a minor pycnocline, corresponding to the shallow thermocline (page 145) appears.

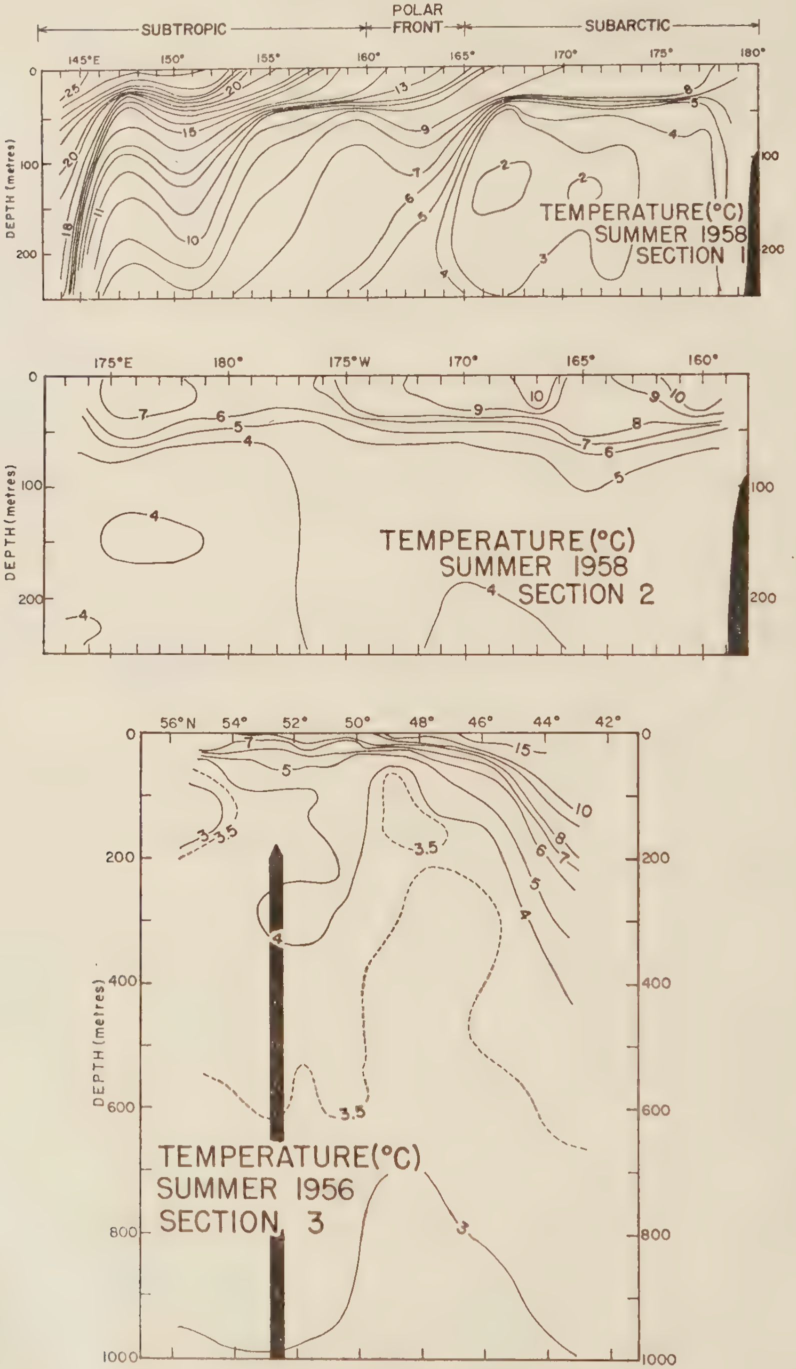


FIG. 27. Temperature, Section 1, summer 1958, Section 2, summer 1958 and Section 3, summer 1956.

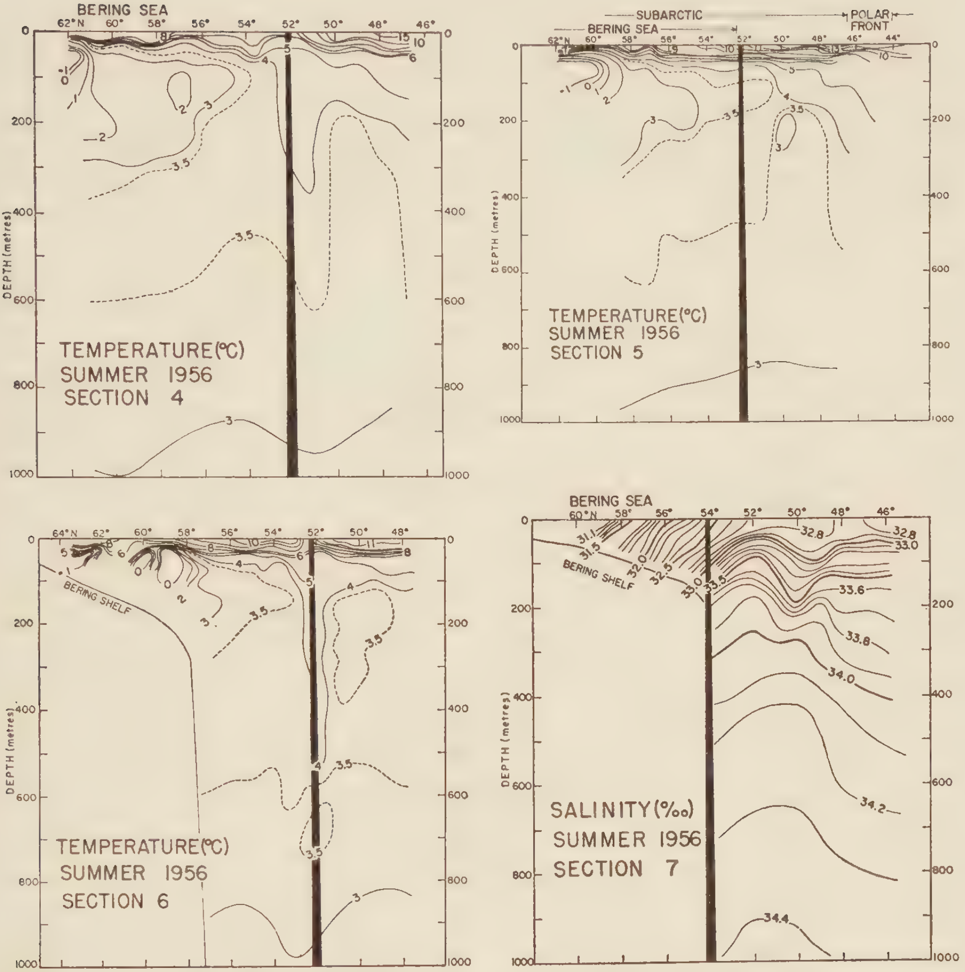


FIG. 28. Temperature, summer 1956, Sections 4, 5, 6 and 7.

This vanishes in winter. A major, permanent, pycnocline occurs in the principal halocline because of the marked increase in salinity. In the lower zone, the density increases gradually into the abyss.

In the Polar Front Region, there can exist throughout a considerable depth (to about 400 m) a succession of minor pycnoclines; these occur because of inversions in either the salinity or temperature structure.

In the Subtropic Region, the warm surface layer, about 10–30 m depth, is isopycnal because of mixing by the Westerlies which are dominant in the region. Below this there is a single, permanent, pycnocline corresponding to the permanent thermocline. In this region the density structure is temperature-dominated.

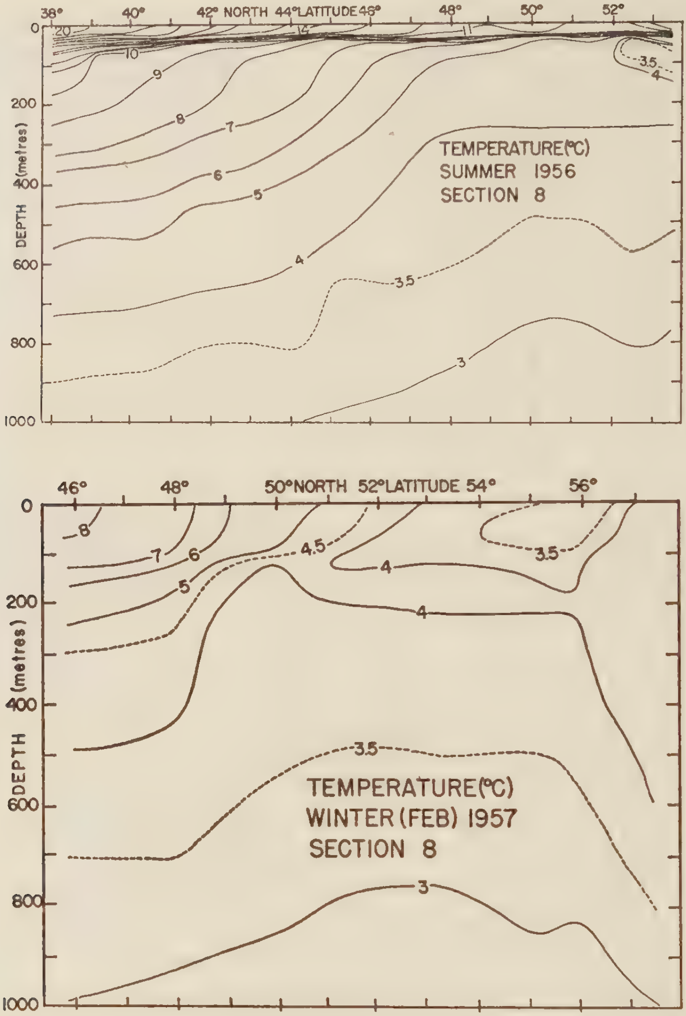


FIG. 29. Temperature, Section 8, summer 1956 and winter (Feb) 1957.

H. DISSOLVED OXYGEN CONTENT OF SUBARCTIC WATERS

The dissolved oxygen content of sea water is one of the basic indicators of marine photosynthetic and respiratory activity—of both flora and fauna—in upper layers. In the euphotic zone (0–50 m) oxygen maxima arising from floral plankton production can appear, given favourable conditions of entrant light, temperature, and dissolved nutrients. Low concentrations or minima of dissolved oxygen at depth (600–1000 m) can be attributed mainly to zooplankton (faunal) respiration and to the decomposition of sinking organic material. The oxygen content in the very deep waters in generally related to non-biological processes.

The solubility of oxygen varies inversely as the water temperature. Also the concentration in the surface waters tends to be near saturation because of the continual agitation by waves. Hence the concentration of oxygen in the surface waters varies seasonally, from a maximum in winter to a minimum in summer (Tabata, 1960). It follows that, in the surface layers of the ocean affected by wind mixing, the oxygen content can often furnish a good indication of the degree of aeration resulting from such mixing.

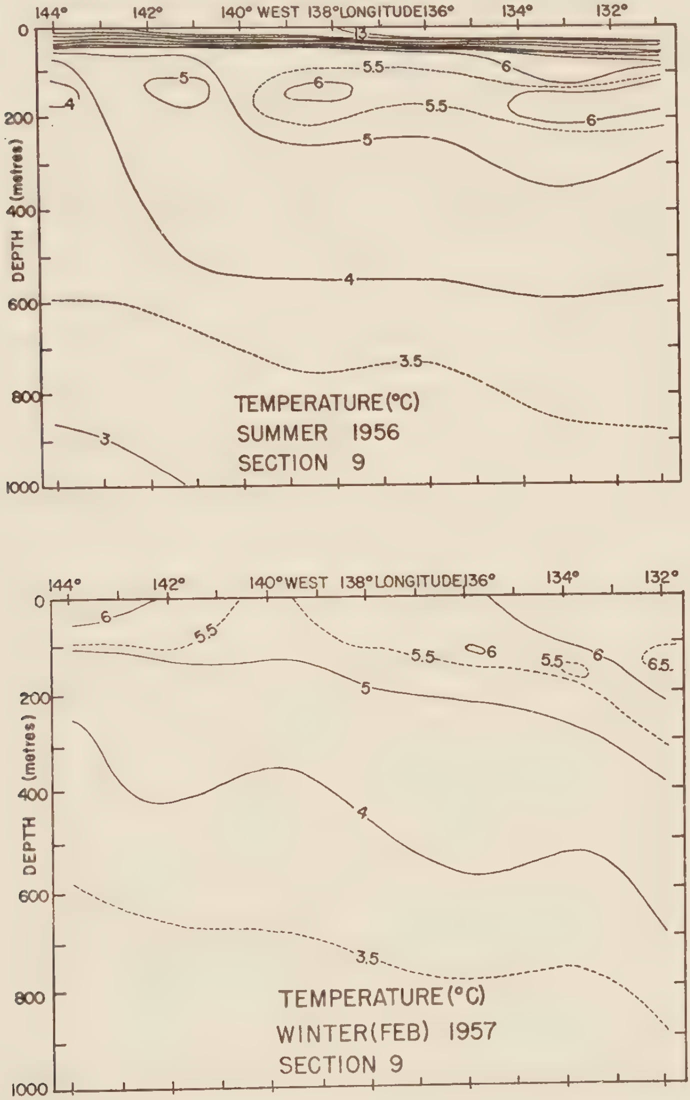


FIG. 30. Temperature, Section 9, summer 1956 and winter (Feb) 1957.

1. Structure of the Dissolved Oxygen Content

Typical winter and summer structures of dissolved oxygen content in the Subarctic Pacific are shown in Fig. 33. The large, quite uniform content (greater than about 0.6 mg-at/l) occurring in winter in about the upper 100 m arises both from the colder water temperature and from the efficient aeration by the strong wind mixing occurring at this time. This iso-oxygen layer coincides with the isohaline and isothermal layer. Below this is a sharp oxycline, extending to about 300 m depth, through which the values decrease to 0.1 mg-at/l. The concentration then usually decreases to a minimum (0.03 mg-at/l) between 800 and 1000 m, then increases slightly with depth to at least 2000 m. In summer the structure appears to be basically the same, except that there exists a fairly marked maximum at a depth of about 30–50 m, presumably arising from phytoplankton photosythesis.

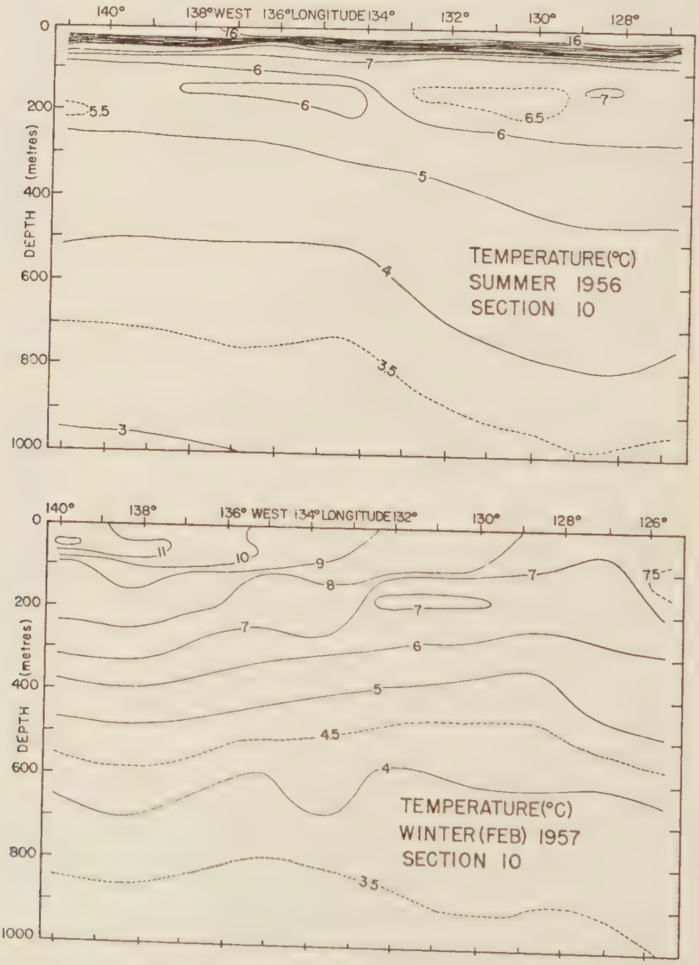


Fig. 31. Temperature, Section 10, summer 1956 and winter (Feb) 1957.

Near the western boundary, the oxygen structure in the Polar Front is often marked by a second maximum (not shown). This occurs because of the presence at depth of highly-oxygenated waters, such as those of the cold Oyashio Undercurrent. In the Subtropic Region, the shallow maximum due to phytoplankton production is rare because of the generally small productivity in this region.

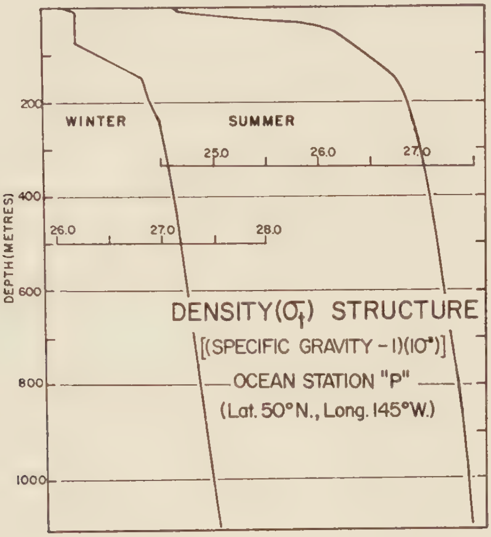


FIG. 32. Density (σ_t) structure at Ocean Station "P", winter and summer.

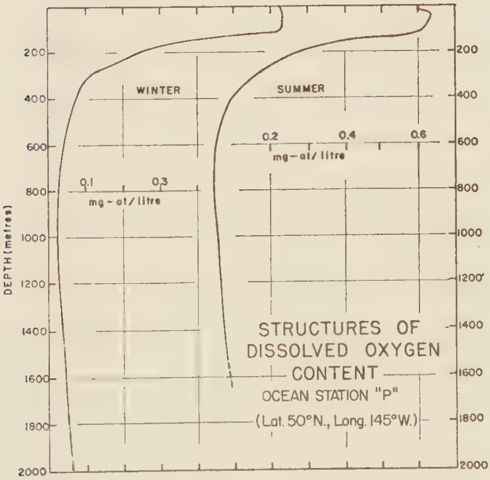


FIG. 33. Structures of dissolved oxygen content at Ocean Station "P", winter and summer.

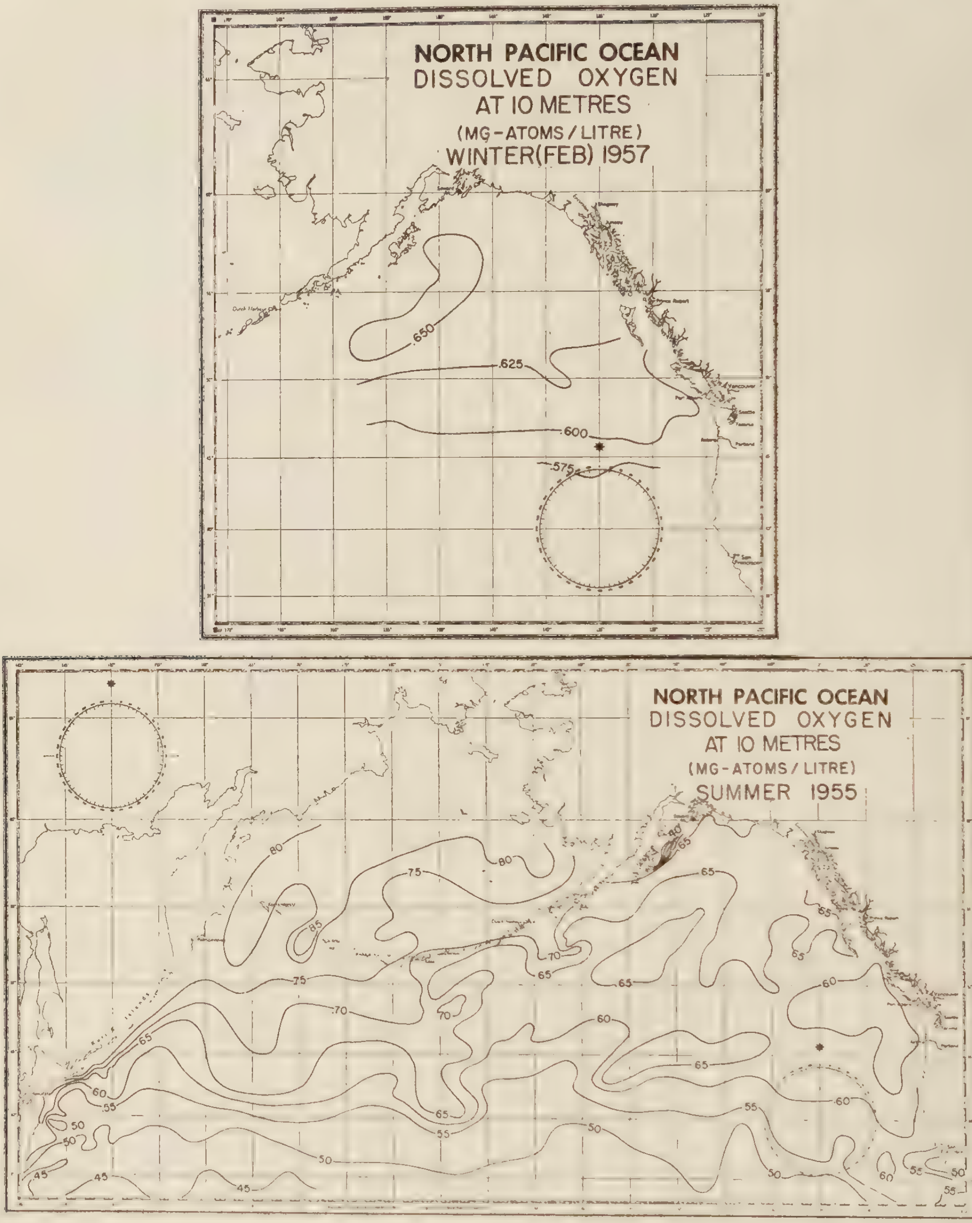

NORTH PACIFIC OCEAN
DISSOLVED OXYGEN
AT 10 METRES
(MG-ATOMS / LITRE)
WINTER(FEB) 1957
.650
.625
.600
.575
NORTH PACIFIC OCEAN
DISSOLVED OXYGEN
AT 10 METRES
(MG-ATOMS / LITRE)
SUMMER 1955
.80
.85
.75
.70
.65
.60
.55
.50
.45

FIG. 34. Dissolved oxygen at 10 metres, winter (Feb) 1957 and summer 1955.

2. Horizontal Distribution of Dissolved Oxygen

A typical horizontal distribution of dissolved oxygen content at 10 metres depth in the Gulf of Alaska in winter is shown in Fig. 34. The data indicate that the isopleths run effectively latitudinally. The content increases northward from the Subarctic boundary to the Alaska Gyre. The highest concentration is associated with the low-temperature water in the dynamic centre of the Gyre.

Comprehensive summer data were obtained throughout most of the Subarctic Region in 1955 (NORPAC) as shown in Fig. 34. There are no comparable data from subsequent surveys. In general the trend of the isopleths was latitudinaly. However, these are not comparable to the corresponding salinity (Fig. 11) and temperature (Fig. 24) distributions, because of the large local variations. The northernmost waters of the region possess the highest surface concentrations, up to 0.8 mg-at/l occurring in the Bering Sea. These high values occur, in part at least, because of the colder water temperatures prevailing in the area. The random variations elsewhere throughout the region, and especially the marked increase about the "cold centre" of the Alaska Gyre might be attributed to biological production.

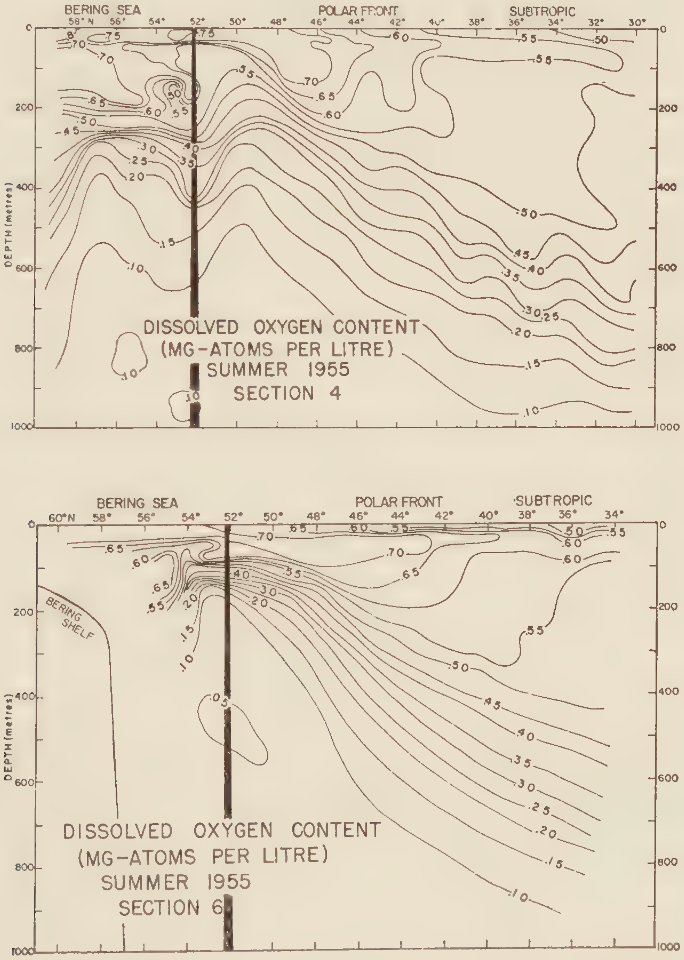


Fig. 35. Dissolved oxygen content, summer 1955, Section 4 and Section 6.

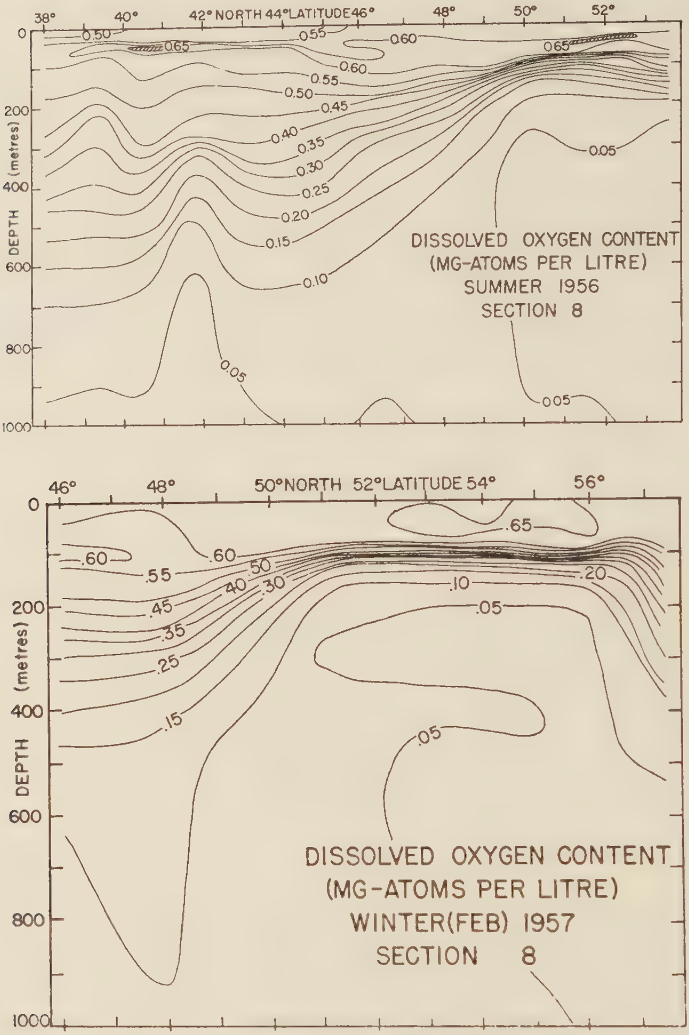


Fig. 36. Dissolved oxygen content, Section 8, summer 1956 and winter (Feb) 1957.

3. Vertical Sections of Dissolved Oxygen

Figures 35 through 38 show the vertical distribution of dissolved oxygen content in several of the sections whose positions are given in Fig. 14. The marked maximum present in summer in the upper layers (and presumably occurring because of biological production) is indicated to be generally present throughout the region. The sharp oxycline, present between about 100 and 300 m depth, is also of general occurrence. In the southern part of the region, the oxycline degenerates, and in the lower zone a nearly linear decrease with depth occurs. In the area of the Alaska Gyre, the lower-zone dome structure, a feature of the distributions of both salinity and temperature, is also present in the oxygen distribution. The oxygen minimum present in the eastern part of the region at depths between 800 and 1000 m (Section 8, Fig. 36), rises in the dome to within 400 m of the surface. The near-surface oxycline remains unchanged within the area of the dome. Sections 4 and 6 in the central portion of the Subarctic (Fig. 35) show decreasing oxygen content with depth. They also show that the isopleths of low concentration in the deep water ascend northward, similar to the isohalines (Fig. 16) and the isotherms (Fig. 28). As shown in Sections 4 and 8 (Fig. 35 and 36) the oxycline is generally present throughout both the Polar Front and Subtropic Regions. It is compressed and becomes shallower towards the north.

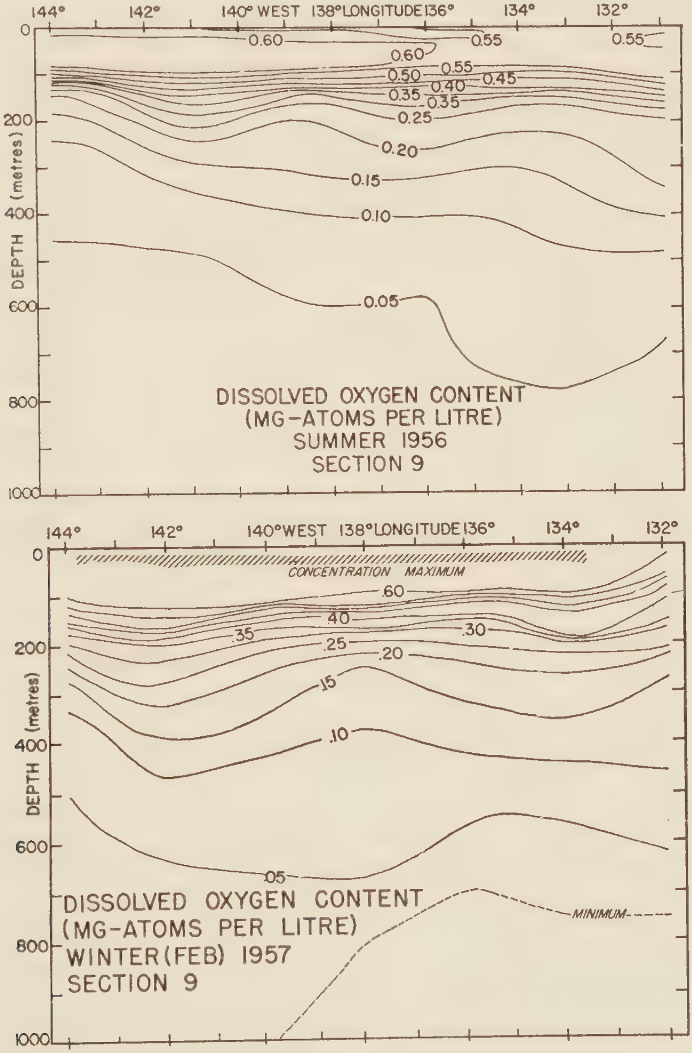


FIG. 37. Dissolved oxygen content, Section 9, summer 1956 and winter (Feb) 1957.

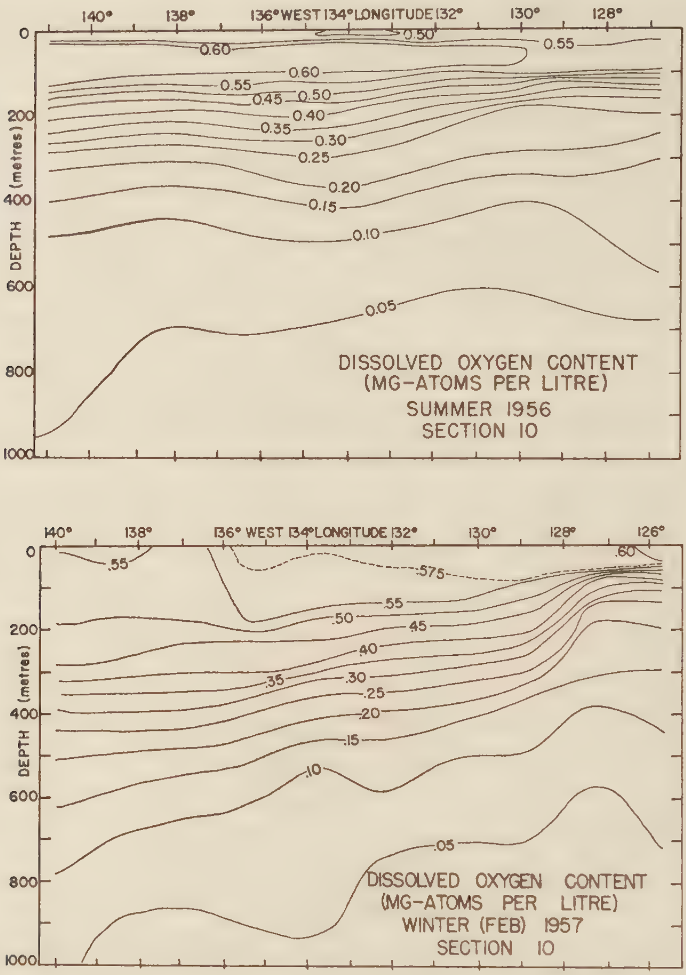


FIG. 38. Dissolved oxygen content, Section 10, summer 1956 and winter (Feb) 1957.

I. TRANSPARENCY OF SUBARCTIC SURFACE WATERS

In addition to the oceanographic variables whose distribution have been discussed, a considerable number of measurements of the transparency or clarity (or the inverse quantity, turbidity) of the surface layers have been made in the Subarctic Region. The measurements have been obtained by means of the Secchi Disc; therefore, they are not by nature highly accurate. Nevertheless, in the open ocean especially, the transparency is inversely related to the abundance of plankton present in the surface layers, and consequently provide a rough quantitative measure of the geographical distribution of planktonic life. Thus transparency measurements are often useful in corroborating the productivity indicated by the relative values of the dissolved oxygen content found in the surface layers. In coastal areas, the usefulness of such measurements to indicate abundance of plankton is often impaired by the presence of terrigenous material brought into the sea by land drainage. In such areas, however, the measurements may serve as an indicator of the volume of fresh water inflow.

The general features of the summer surface layer transparency in the Subarctic Region are shown in Fig. 39 and 40 (1955 through 1958).

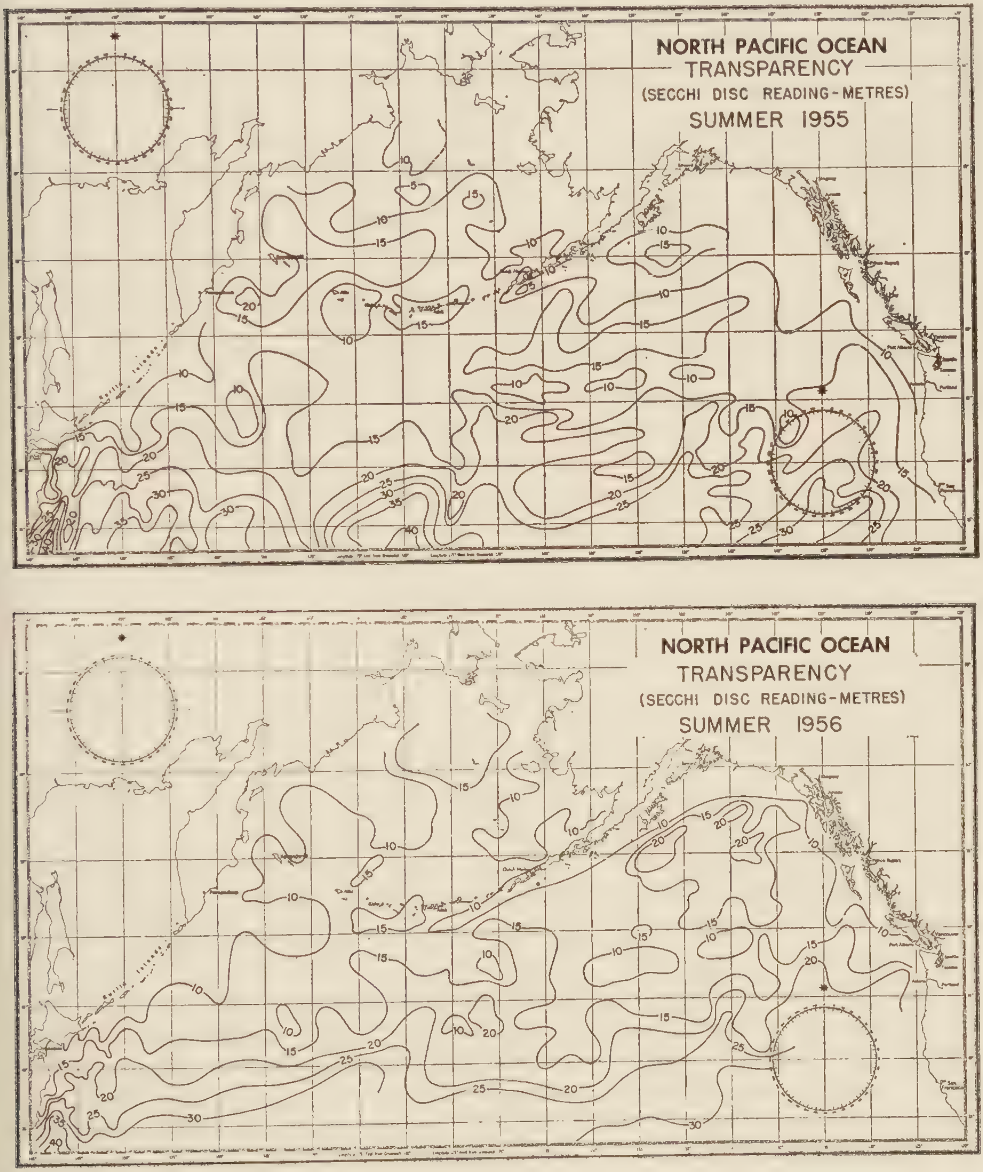

NORTH PACIFIC OCEAN
TRANSPARENCY
(SECCHI DISC READING-METRES)
SUMMER 1955
NORTH PACIFIC OCEAN
TRANSPARENCY
(SECCHI DISC READING-METRES)
SUMMER 1956

FIG. 39. Transparency, summer 1955 and summer 1956.

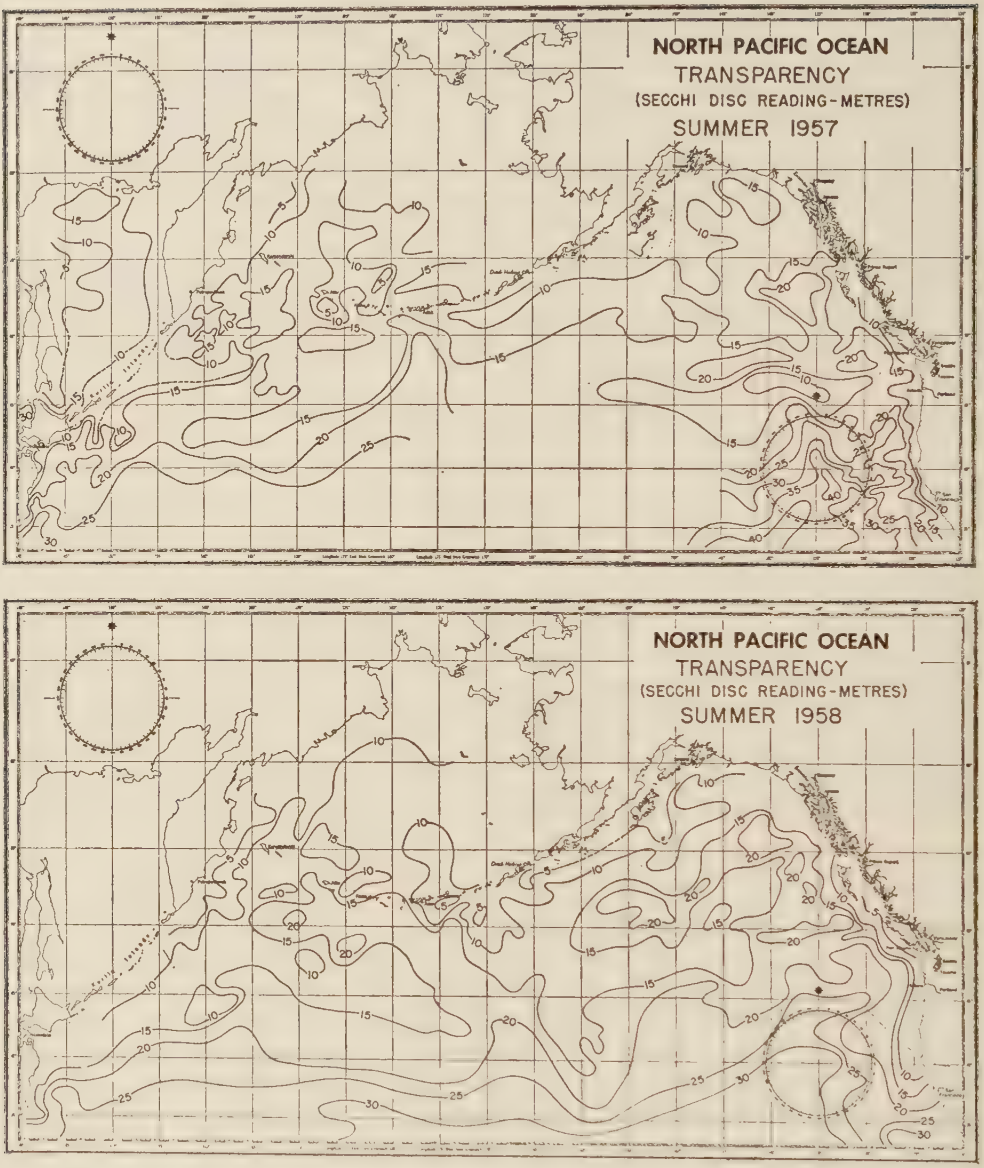

NORTH PACIFIC OCEAN
TRANSPARENCY
(SECCHI DISC READING-METRES)
SUMMER 1957
NORTH PACIFIC OCEAN
TRANSPARENCY
(SECCHI DISC READING-METRES)
SUMMER 1958

FIG. 40. Transparency, summer 1957 and summer 1958.

Marked, and for the most part apparently random, variations of transparency are very evident throughout the region. This condition is presumably indicative of a "patchiness" in the distribution of planktonic life. In the waters of the Oyashio the limit of visibility of a Secchi Disc is usually less than 10 m. This low transparency is in keeping with Oyashio's reputation as a rich area of planktonic life (page 167). The low-salinity coastal waters are even more turbid, visibility being generally much less than 10 m. This fact is due, in some measure at least, to silt. Localities of relatively high transparency (15–20 m) approximate in position the central high-salinity cores both of the Bering Sea and of the Alaska Gyre.

In the Polar Front Region, there appears a marked southward increase in transparency, visibilities to 30 m being common (and some as great as 45 m being obtained occasionally). These values indicate that a smaller amount of plankton is present in the Subtropic Region. A belt of relatively clear water (Secchi reading greater than 20 m) present between Ocean Weather Station "P" (Lat. 50° N, Long. 145° W) and the American coast, provided further evidence of unusual oceanographic conditions (page 171) in 1957 and 1958 in that area (Tully *et al*, 1960).

Generally speaking, in the open ocean, transparency appears to be proportional to salinity, and inversely proportional to concentration of plankton.

J. OTHER IMPORTANT FEATURES OF THE SUBARCTIC REGION

1. Major Currents of the Subarctic Region

Two major permanent current systems lie entirely within the Subarctic Region (page 120) (Fig. 7). Both currents are affected to some degree by seasonal (non-persistent) intrusions of water from the Polar Front into the Subarctic. Characteristics of the two currents are summarized briefly:

(i) The Oyashio (Japanese: "Oya"—parent, "shio"—current) (Fig. 7).

Considered in its most restricted sense, it is the current flowing southwest from the Kamchatka Peninsula to the northern Japanese islands (Lat. 50° N, to 40° N). Transport is between 7,000,000 and 10,000,000 m^3 per second, and is composed, at the southern extremity, of equal amounts of water from three sources (Sugiura, 1957):

East Kamchatka Current—This current arises from water which has circulated anti-clockwise around the Bering Sea and has been greatly affected by the appearance (in the summer) of ice-melt water (primarily from the Gulf of Anadyr) and of land drainage from the East Kamchatka coast. This is modified in turn both by upwelling and by the North Kurile Warm Current (page 171).

East Sakhalin Current—This is water flowing along the western side of Okhotsk Sea. It too is composed of ice-melt and land drainage water and is affected by upwelling. Flow of this water out through the middle Kurile Islands continues throughout the year (page 150).

Oyashio Gyre—Water recirculated in this cyclonic gyre is present off the Kurile Islands between about 150 and 155° east longitude.

Major Characteristics of Oyashio. The temperature is low, generally less than 9° C. Salinity is low, less than 33‰. The depth of the current is 200–400 m. The speed is between 0.3 and 1 knot. The nutrient content is high. The Japanese name may originate from the fact that the current is a rich source of food for marine life. The transparency is low; the Secchi Disc visibility is usually less than 15 m.

A major portion of the Oyashio turns east and forms part of the West Wind Drift. A minor part forms the Oyashio Undercurrent which moves south and southwest under the Kuroshio. It is believed that the strength of the Undercurrent is determined primarily by meteorological conditions (page 173).

(ii) The Alaska Stream and Its Extension.

The Alaska Stream is the narrow intense stream flowing along the southern coast of the Alaska Peninsula from Kodiak Island to Unimak Pass (Long. 150° W to 160° W). Its speed is of the order of one-half knot. The transport includes most of the flow in the Alaska Gyre plus the northern transport adjacent to the Canadian Coast. In summer, the total transport is about 17×10^6 m^3 per second and flow occurs to at least a depth of 2000 m (Bennett, 1959). Intensification characterizing the stream is probably due to the conservation of absolute vorticity through changing latitude. It appears, from results of drift-bottle releases (Dodimead and Hollister, 1958), that a portion of the Alaska Stream recirculates around the Alaska Gyre at least occasionally, although this is not readily apparent in the geostrophic circulation (Fig. 5 and 6). The Alaska Stream Extension is the continuation of the Stream westward past Unimak, and may be termed the *Return Flow* (of the West Wind Drift) out of the Gulf of Alaska. The Extension develops westward in the spring and summer, reaching furthest west about August. The development is due to the increase of land drainage from the southern coast of Alaska during the spring and summer months. Water moves out to the end of the Aleutian Chain, successive portions moving through the island passes into the Bering Sea. Extension water moving through the Aleutian passes is affected to a degree by the (seasonal) South Aleutian Warm Current.

Major characteristics of the Alaska Stream. The temperature of both the current and its extension is relatively warm throughout the year. The salinity is low throughout (especially in summer because of land drainage) but increases along the line of flow due to entrainment (page 169) and mixing.

2. Cold Cores

In the Subarctic Region, there are several localized areas in which the upper-zone water exhibits temperatures markedly less than those of the surrounding water, during part or all of the year. These areas are depicted in Fig. 41 and are termed "Cold Cores". They are assumed to be formed by a number of factors acting either singly or together, such as: southward intrusions of cold water into an area of warmer water, the formation of ice-melt water, upwelling, and the movement of deep zone water into the upper layers.

The Core numbered (1) appears to be a manifestation of general southward intrusions of branches of the cold Oyashio Current. One such intrusion, presumably generated by meteorological conditions, is discussed more fully on page 173. Cores (3), (4), and (5) are formed by ice-melt water released in the summer. The tendency to lower temperatures is also enhanced by the upwelling associated with the south and southwest winds prevailing at this time. Such upwelling

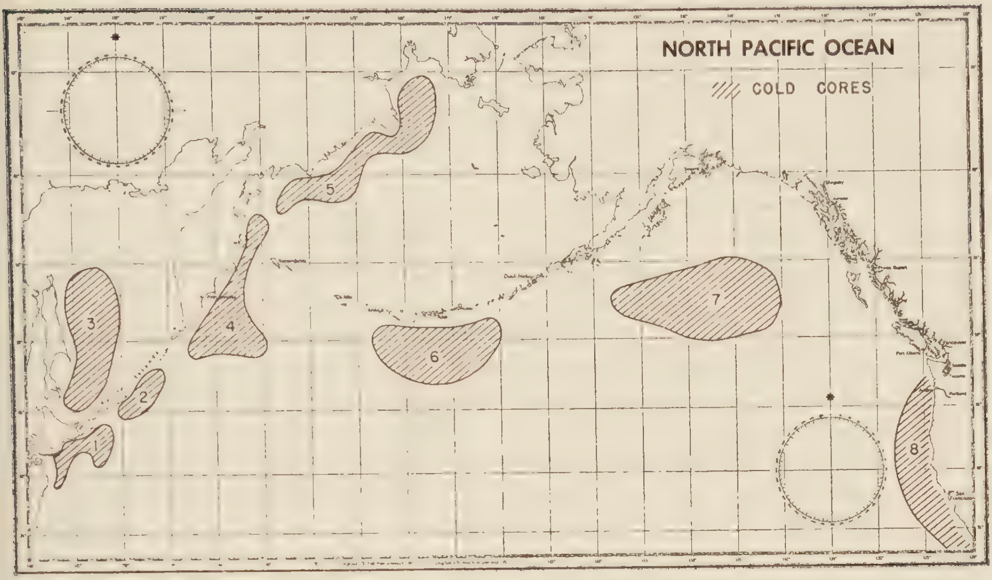


FIG. 41. Cold cores.

draws water to the surface from modest depths only, usually less than 200 m. Core (8) off the Oregon and California coasts between Lat. 30 and 45° N occurs because of the prevailing northwest winds of spring and early summer, which cause upwelling during the period from March to July.

Cores (2) and (7) occur near the dynamic centre of the Oyashio and Alaska Gyres respectively. In the Alaska Gyre core, the one most intensively studied, several important features have been noted. The isolines of all properties in the deep water exhibit at all times pronounced domelike configurations (page 162). However, the typical subarctic structure (Fig. 8) is present and continuous in the dome. Both the principal halocline and the thermocline exist there. The depth of the upper zone is slightly less than that in the surrounding area (Dodimead, 1961).

The typical Subarctic structure is similar to that present in the coastal inlets of British Columbia. In these inlets, velocity differences between upper and lower zones gives rise to a shear between them. This shear apparently provides the energy for the preferential upward transfer or *entrainment* of deep water into the upper zone (Tully, 1958). In this concept, the shear zone is in the transition zone (the principal halocline).

It appears, both from the continuation of the typical Subarctic structure through the area of the Alaska Gyre and from the horizontal distribution of properties in the area, that sub-halocline water is entrained into the upper zone in a manner essentially similar to that in British Columbia inlets (Tully and Barber, 1960). Tully (private communication) contends that the most intense entrainment appears to occur in the dynamic centre of the Gyre. Presumably, a localized centre of entrainment is also present in the Oyashio Gyre. The upper zone in the Subarctic can be considered to be a combination of fresh water and entrained sub-halocline water, modified by "surface" effects such as evaporation, freezing, wind mixing, etc.

The cold core (6) occurs between two opposing flows, the Alaska Stream Extension and the West Wind Drift; the associated dynamics are probably responsible for the presence of the core.

3. Replenishment of Water to the Subarctic Region

The circulation system of the Subarctic (page 127) indicates that water is lost from the region by two avenues. One is the prevailing northward flow through Bering Strait; the other, and more important, is the southward deflection of part of the West Wind Drift into the Subtropic Region. It appears that about three fifths of the upper zone waters may be lost on the round trip (Tully and Barber, 1960).

The formation of sea ice has been mentioned as occurring in winter in both the Okhotsk and Bering Seas (page 147). However, the salinities of the surface layers are so low, due to dilution, that the density of the cold saline water remaining is still less than that generally present at quite modest depths in the Subarctic Region. Deep water is therefore not formed by convective overturn (and indeed, is not produced at all) in the Subarctic Pacific.

Masuzawa (1960) studied the Oyashio Undercurrent off the coast of Japan and concluded that in this limited region (Cold Core (1), Fig. 41) the Oyashio water descended to about 1100 m depth. Below this, the abyssal waters were generally rising. However, this observation bears on the genesis of intermediate waters in the Polar Front and Subtropic Region, which has not been discussed in this review. It in no way detracts from the conclusion that deep water is not produced in the Subarctic Region as defined here (Fig. 1). The region thus differs from others such as the North Atlantic and the Antarctic, in which large quantities of deep and bottom water originate at the surface. Any renewal, therefore, of deep water which has been entrained or upwelled into the upper zone and subsequently lost from the Subarctic Region because of the persistent circulation, can only occur by deep inflow from south of the region, and by subsequent upwelling or entrainment into the upper zone.

In his recent study, Bennett (1959) indicated that at least one source of persistent deep flow into the Subarctic exists. It appears that below the halocline (200 m) down to at least 2000 m depth, water persistently intrudes into the Gulf of Alaska from the southeast and circulates around the deep basin.

4. Intrusions in the Subarctic Region

Several non-persistent flows of water occur in the upper few hundred metres, and influence the persistent circulation quite markedly. In addition, non-persistent movements are presumably present in the deep and abyssal waters; however, nothing is known about their characteristics up to this writing. It is theorized, however (page 174), that the movements in the upper layers originate primarily from the meteorological conditions that occur in the Subarctic Region and its surroundings.

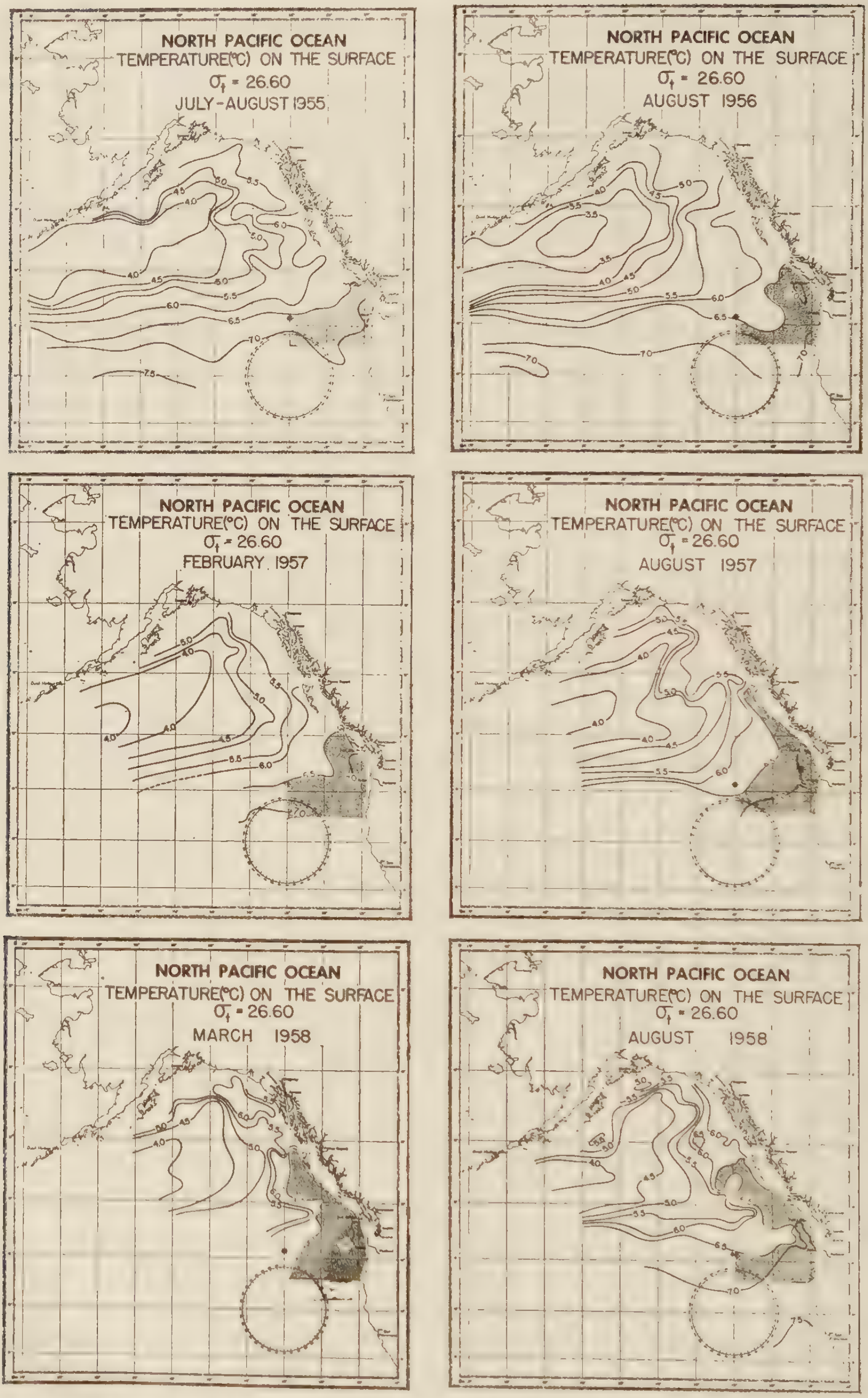
Two (warm) intrusions from the south occur during the summer period. These weak surface currents, the South Aleutian Warm Current and the North Kurile Warm Current, are probably due to summer strengthening of the Kuroshio and the coincident weakening of the Oyashio. Commencing in May they develop rapidly. They decay during the following September and October. The South Aleutian Warm Current is a northward intrusion from about Lat. 45 to 50° N, between about Long. 170 and 180° W (Fig. 7). It shifts somewhat to the west during the course of the summer. The North Kurile Warm Current occurs east of the North Kurile Islands and off Kamchatka, between about Long. 160 and 165° E. Some of the (relatively) warm saline water of these currents cools sufficiently to subside and form mesothermal water (page 150). The currents, although transitory in nature, affect the overall circulation of the Subarctic to some degree. A part of the South Aleutian Current mixes with the Alaska Stream Extension (page 168), and enters the Bering Sea through passages in the Aleutian Island Chain. The water entering the Sea of Okhotsk is composed of water originally from the East Kamchatka Cold Current and thus is modified by both the North Kurile and South Aleutian Warm Currents.

While these warm currents recur to some extent every year, their intensity appears to vary markedly with the years. For example, summer surface water temperatures in the Western Bering Sea were found during the period 1954–58 to be warmest in 1957 and colder in 1955, 1958, and 1956, respectively (Fig. 14 and 25). The variation in these temperatures is presumably due primarily to fluctuations in the intensity of the North Kurile Warm Current.

Other northward intrusions, whose intensity appears to vary more slowly with time than those just mentioned, occur at both eastern and western sides of the Subarctic Region. The eastern, the more massive one, occurs between about Long. 150° W and the North American Coast. The western one occurs off the northeastern coast of Japan at about Long. 145° E.

The North American Intrusion has been studied by Tully *et al.* (1960). In 1955 and 1956, the division of the West Wind Drift occurred off the American Coast between Lat. 46 and 48° N, well within the Subarctic Region. In 1957 it was noted that the division had shifted, since the beginning of the year, about 200 miles southward. Thus more of the relatively warm (Polar Front) water entered the circulation of the Alaska Gyre. The geopotential topography indicated that the mid-ocean currents tended more northward than in previous years. This alteration in flow was confirmed by drift bottle releases. At the same time, transparency measurements indicated that, on the surface at least, very clear water indicative of Polar Front water appeared in the general area of the intrusion.

The warming was found to extend to about 500 m depth. This fact signifies that the phenomenon resulted principally from the influence of advection and not from seasonal heating and cooling effects, which are not significant much below a depth of about 100 m (Tully *et al.*, 1960). Fig. 42 shows the variation in the extent of the intrusion during six successive surveys in the eastern Subarctic throughout the period 1955–58. In this Figure, the temperature distribution on the surface of constant density $\sigma_t = 26.60$ was examined. This surface is



NORTH PACIFIC OCEAN
TEMPERATURE(°C) ON THE SURFACE
σ_t = 26.60
JULY-AUGUST 1955

5.0
5.5
4.5
4.0
6.0
5.0
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5

NORTH PACIFIC OCEAN
TEMPERATURE(°C) ON THE SURFACE
σ_t = 26.60
AUGUST 1956

5.0
4.5
4.0
3.5
3.5
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.0
7.0

NORTH PACIFIC OCEAN
TEMPERATURE(°C) ON THE SURFACE
σ_t = 26.60
FEBRUARY 1957

5.0
4.0
5.5
5.0
4.0
4.0
4.5
5.5
6.0
6.5
7.0

NORTH PACIFIC OCEAN
TEMPERATURE(°C) ON THE SURFACE
σ_t = 26.60
AUGUST 1957

5.0
4.5
4.0
5.0
5.5
4.0
4.0
4.5
5.5
6.0

NORTH PACIFIC OCEAN
TEMPERATURE(°C) ON THE SURFACE
σ_t = 26.60
MARCH 1958

6.0
5.0
4.5
4.0
5.5
5.0
6.0
5.5

NORTH PACIFIC OCEAN
TEMPERATURE(°C) ON THE SURFACE
σ_t = 26.60
AUGUST 1958

5.0
5.5
3.5
5.0
4.0
4.5
5.5
6.0
6.5
5.0
5.5
6.0
6.5
7.0
7.5

FIG. 42. Temperature on the surface of σ_t = 26.60, July–August 1955, August 1956, February 1957, August 1957, March 1958 and August 1958.

known to lie between 125 and 225 m depth in the area of interest. Thus it is always below the depth of seasonal influence. The shaded portions show the progressive increase of the area of water warmer than 6.5°C. The relative strength of the intrusion was, by years, 1958 (strongest), 1957, 1955 and 1956 (weakest).

The intrusion of warm water northward along the Japanese coast was reported by Uda (1938a, 1960) and Takenouti (1960). By contrast with the sequence off the Canadian coast, it was 1955 (strongest), 1956, 1957, 1958 (weakest). In addition, the weakening of this intrusion appeared to be accompanied by the simultaneous development of a countering southward movement of colder water. This occurrence was caused by variation in strength of the southward-flowing Oyashio Current and Undercurrent.

A fact readily noticeable is the phase difference of occurrence of the various intrusions. There appears to be a lag of about 3 years between the extremes of the intrusions in the western and eastern Subarctic respectively.

A relatively simple explanation, one which appears to relate firmly the strength of the intrusions in the Subarctic and the meteorological conditions in the region and its surroundings, can be put forward. The explanation avails itself of the fact that wind speed (W) is virtually proportional to the square root of the difference between "core-pressures" of opposing barometric high- and low-pressure cells in the atmosphere. Therefore,

$$W = k_1 \sqrt{P_H - P_L} \qquad \ldots (1)$$

P_H = core-pressure of high-pressure cell

P_L = core-pressure of low-pressure cell

The speed (V) of the current generated by the resulting wind stress is in turn proportional to the wind speed,

$$V = kk_1 \sqrt{P_H - P_L} = KW \qquad \ldots (2)$$

where K is the "wind factor", having a value between 0.02 and 0.03. The wind-induced current in the sea is, to a first approximation, parallel to the isobars of atmospheric pressure. (The direction of the wind at sea level is about 30° to the left of the isobars, while the wind driven current is about 30° to the right of the wind), (Uda, 1955).

In Fig. 43 are shown average monthly differences in core-pressure between the various cells influencing meteorological conditions in the Subarctic Region (page 122, Fig. 2 and 3). The period covered is from 1955 to 1958 inclusive; the quantities plotted should be proportional to the square of the resulting wind speed. Fig. 43(1) shows the core-pressure difference between the Siberian High and the Aleutian Low; the resulting winds must tend to affect conditions on the western side of the Subarctic Region. The area under the "Pressure-difference versus Time" curves is taken to be indicative of the transport directly induced by wind. The transport appeared in this case to be southward most of the year, the effect being especially marked during the winter months. The annual transport increased throughout the 4-year period, reaching a maximum in the winter of 1957–58. This fact is presumed to account for the progressively

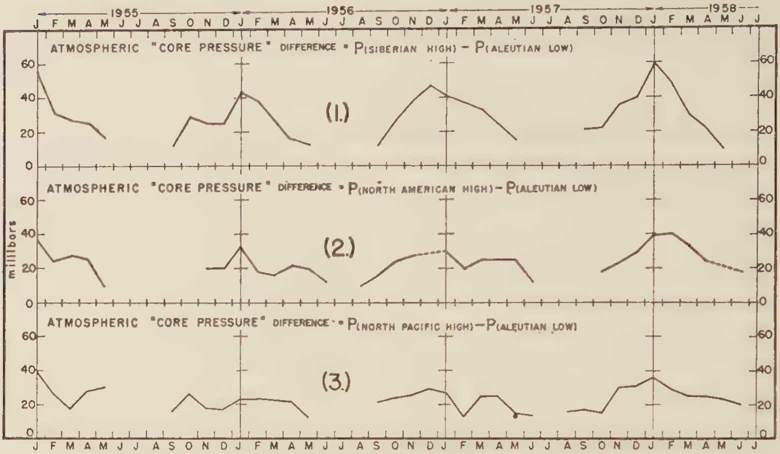


FIG. 43. Atmospheric "core pressure" differences.

colder water temperatures encountered, in succeeding summers, off the northeast coast of Japan. (It also gives a measure, therefore, of the weakening of the warm intrusion.)

Figure 43(2) shows core-pressure differences between the North American High and the Aleutian Low, and Fig. 43(3) shows those between the North Pacific High and the Aleutian Low. The differences in Fig. 43(2) which would give rise to effectively northward flow in the eastern Subarctic, were at a maximum in winter or early spring. The effect was progressively greater through the 4-year period, and especially so during the last three of the years. The differences shown in 43(2) also lead to progressively greater northward transport into the eastern Subarctic, especially during spring. Therefore, presumably because of the combination of these two effects, the temperatures in the upper layers of the eastern Subarctic reached a maximum in 1958. In addition, the *relative* variation in transport during the 4-year period was much greater in the eastern than in the western Subarctic. This fact could explain the much more marked warming occurring in the eastern area.

The warm (northward) intrusions occurring annually in the central part of the region (the South Aleutian and the North Kurile Warm Currents) can be explained reasonably on the basis of transport induced by the pressure difference between the North Pacific High and the Aleutian Low (or, in the absence of the latter cell, by the pressure distribution in the North Pacific High itself). Such transport is present during the spring and early summer (page 00). The correlation between the annual variations in the pressure differences (Fig. 43(3)) and in the strength of the intrusions is not as marked as in the cases previously discussed. However, a pronounced minimum in the northern extent of the intrusion of 1956 is matched by a corresponding minimum in the pressure differences.

Recently the author has studied the non-seasonal fluctuation of sea-surface temperature, along the zone between 35 and 55° N latitude, across the Pacific

Ocean (Uda, 1960). This was based on the data contained in the publication "Mean atmospheric pressures, cloudiness, and sea surface temperature of the North Pacific Ocean and neighbouring seas (1911–1941)" (Imperial Marine Observatory, Kobe). He concluded that the sequence of occurrence of warmer and cooler-than-normal surface waters on the western side of the Pacific was opposite in phase to the occurrences on the eastern side.

On the western side, the minima of surface seawater temperatures occurred in 1913, 1923, 1926, 1934 and 1941. These coincided with maxima on the eastern side of the Pacific. On the western side, maxima of surface seawater temperatures occurred in 1916, 1930, 1933, and 1937. These corresponded to minima on the eastern side. The anomalies alternate from west to east across the ocean.

This converse relation between the occurrence at the western and eastern sides of the ocean of warm and cool conditions is evident in the zone between 40 and 50° N latitude, and is most obvious during the months of February, May and August. The sequence of warm and cool years is similar in the eastern Pacific and eastern Bering Sea from 40 to 55° N latitude.

Superimposed on these variations during the period 1911 to 1941 there was a general warming of 1 to 4 C° in the North Pacific waters. This was especially notable in the western and eastern sides during winter and spring. In summer the warming was most notable in the central part of the ocean, particularly in the Polar Front.

This alternating behaviour is attributed to fluctuations in the relations between the three atmospheric pressure centres (Fig. 43). In winter the Oyashio is accelerated by the monsoons generated by the pressure gradient between the Siberian High and the Aleutian Low. This cold outflow from the Okhotsk and Bering Seas becomes dominant when the pressure difference is extreme. This condition retards the northward progress of the warm Kuroshio waters and diverts them eastward into the trans-Pacific drift. On the eastern side of the ocean, the northward transport into the Gulf of Alaska depends on the pressure difference between the Aleutian Low and the North American High.

The author proposes a "pulsation" theory such that these two major gradients are intensified periodically. Hence the wind stresses are intensified and in consequence the system of gyres, which constitutes the Subarctic circulation, is intensified. This mechanism causes the intrusions. The sequence of variations is not due to a planetary wave system. Rather it is due to a quasi-stationary pulsational wave with fluctuating amplitude due to topographically confined or boundary-conditioned gyres.

Professor J. Bjerknes (1960) recently presented an interesting paper based on data observed during 1890 through 1933. He shows conditions in the North Atlantic Ocean similar to those we have observed in the North Pacific. Previously, Rodewald (1957) showed that the trends of warming and cooling occurred concurrently along the western sides of the North Pacific and North Atlantic Oceans.

ACKNOWLEDGMENTS

The data were examined and this paper was drafted while I was a visiting scientist at the Pacific Oceanographic Group (Nanaimo, B.C.) of the Fisheries Research Board of Canada, from September 1958 through June 1959. The assistance of the staff in providing material, references, and many of the concepts is acknowledged. Mr R. L. Johnston prepared the illustrations from the original sketches. Dr L. F. Giovando prepared the English manuscript from my notes, and a series of seminars (Uda, 1959) which I presented in Nanaimo. Their very considerable contribution is acknowledged. Thanks are also given to the Director of the Nanaimo Biological Station, Dr A. W. H. Needler, and the Oceanographer-in-Charge, Dr J. P. Tully, for the facilities provided and the opportunity to make this study.

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Apparatus for Measuring the Energy Input in Cutting Fibers of Fish Muscle[1]

By Hans Buttkus[2]

Fisheries Research Board of Canada
Technological Station, Vancouver 8, B.C.

ABSTRACT

The construction and operation of an apparatus for measuring the amount of energy expended in cutting muscle fibers is described. The measured energy permits a quantitative comparison of the toughness of different samples. Measurements on a model system of paraffin wax show a variation of ±5%. With muscle fibers of raw and cooked salmon, lingcod and beef, the variation in these measurements was sometimes as high as ±20%.

INTRODUCTION

The influence of different treatments, particularly in connection with stored frozen fish, in occasioning increased organoleptically detectable toughness in the muscle tissue, is now well-known (Amlacher, 1961; Dingle and Dyer, 1961). In a previous paper (Buttkus and Tarr, 1962) the need for a reliable method for measuring texture changes such as occur in *rigor mortis* development and protein denaturation caused by freezing was emphasized. Devices which have been developed in order to determine objectively the texture changes in beef muscle have not been found suitable for fish muscle in which the fibers are shorter (Love, 1958, 1960; Nemitz *et al.*, 1960). The most promising method of measuring increased toughness in frozen fish muscle appears to be the "cell fragility" technique recently developed by Love (Love, 1962; Love and Mackay, 1962). The present report describes a device with which the resistance of muscle fibers to a cutting force can be measured.

APPARATUS AND METHOD

The mechanical portion of the apparatus is shown in Fig. 1. A stainless steel plunger is attached to a balanced aluminum beam. The lower portion of the plunger is positioned in the hole of the stainless steel platform, both of which are machined to finest tolerance, permitting free movement of the parts yet providing shearing action. One end of the sample (see below), is inserted into the horizontal hole through the plunger. When the platform, driven by a synchronous motor, rises at constant speed, the sample is sheared at constant rate. The changing resistance with which the sample opposes the shearing force is transmitted via the beam and the brass chain to the shaft of the me-

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[1] Received for publication September 18, 1962.

[2] Present address: University of California, Davis, Calif., U.S.A.

J. Fish. Res. Bd. Canada, **20**(1), 1963.
Printed in Canada.

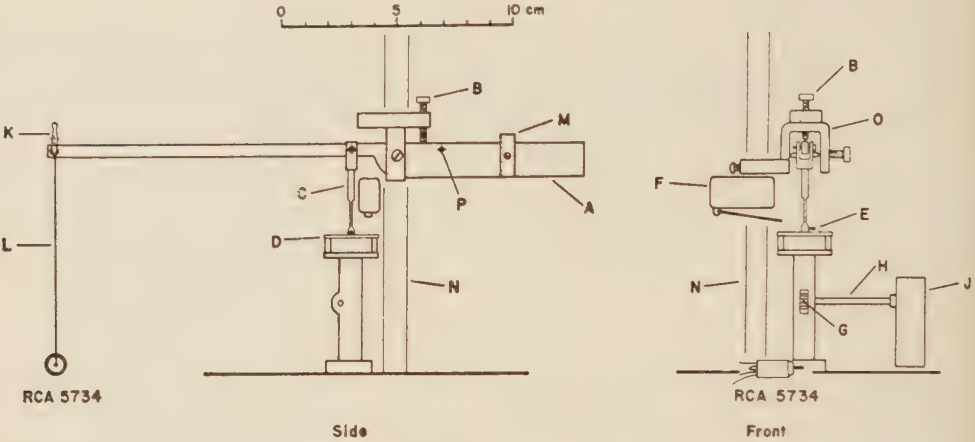

FIG. 1. Mechanical section of fiber shear apparatus: *A*. Aluminum beam; *B*. Set screw; *C*. Stainless steel plunger containing a hole 1.7 mm in diameter into which a portion of the sample is inserted for measurement; *D*. Stainless steel platform (1 mm thick) with an opening through which the lower portion of the plunger moves during operation; *E*. Sample inserted into horizontal hole of plunger, ready for measurement; *F*. Micro switch; *G*. Brass spur gear, 10 teeth, pitch 48, to drive brass rack with attached platform in upward direction; *H*. Driving shaft between spur gear and synchronized motor; *J*. Synchronized motor, 5 W, 1 rpm, right, clutch 1-way (Haydon, Torrington, Conn., U.S.A.); *K*. Small alligator clamp holding brass chain to lever; *L*. Brass chain attached to the shaft of the Mechano-Electronic transducer RCA 5734; *M*. Rider weight for balancing lever; *N*. Support for apparatus; *O*. Adjustable lever support; *P*. Position for attachment of weights during calibration.

chanical input transducer tube RCA 5734 (Radio Corporation of America, 1948). After the sample has been cut and the platform has reached a certain height, a micro-switch stops the motor drive. The platform is then returned to its initial position and is prepared for the next sample by cleaning off bits of muscle fiber and by lubricating plunger and platform with glycerol.

Adjustment of the force recording circuit is accomplished as follows (Fig. 1). First, the beam (A) is balanced and the brass chain (L) is tightened lightly by means of screw (B). The wheatstone type bridge circuit, Fig. 2, is then balanced electrically by adjusting the Beckman millivolt recorder (mV) to zero (base line) with the variable resistor 10 K. The apparatus is thus ready for operation.

Calibration is carried out with weights from 10–100 g which are hung on the beam at position P (Fig. 1). The response in millivolts to the attached weights is linear and the rate of shear during the cutting process is constant. The area under the curve (A) is therefore directly proportional to the work (W) required in cutting a sample; $W = KA$. The constant K, whose value must be rechecked during operation, is calculated as follows: since the linear speed of the platform is 1.5 cm/min and the chart speed of the millivolt recorder is 11.00 cm/min, 0.734 cm on the chart is equivalent to a movement of 0.1 cm by the platform. The height of the ordinate is found by attaching a 50.0-g weight to the beam. The rectangular area thus described, (b) of Fig. 4, then represents the work ($W = Fs = 50 \times 980 \times 0.1$) of 4900 ergs. The weight of this area when cut out

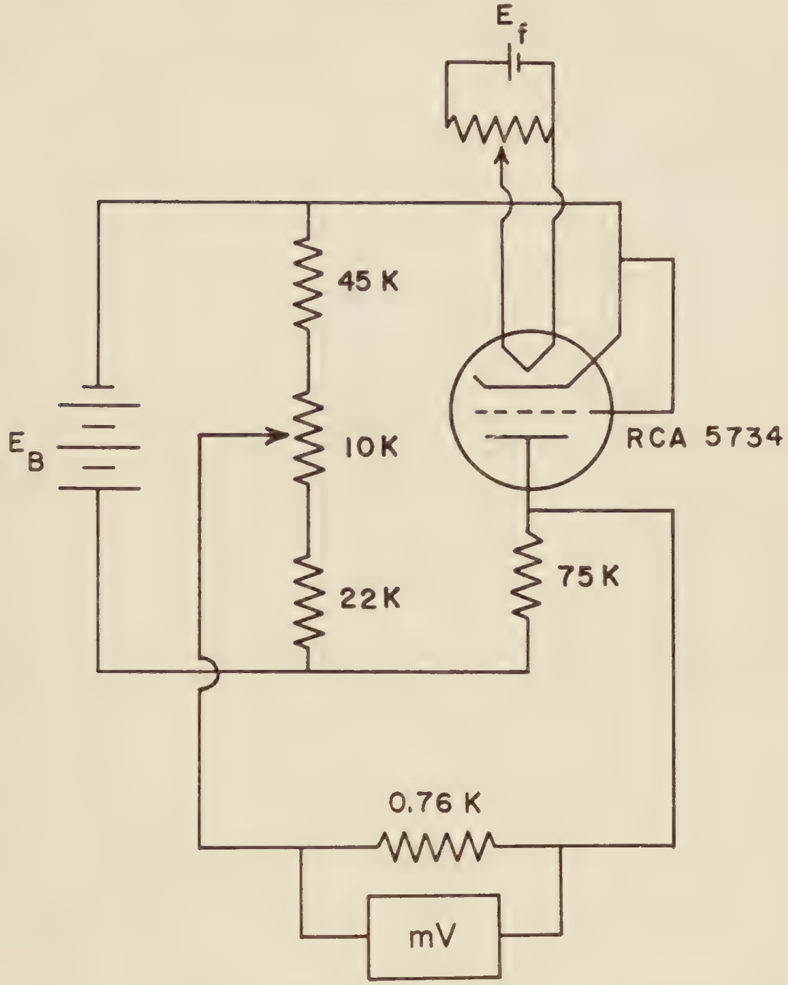

FIG. 2. Force–distance recording circuit of fiber shear apparatus: E_B = 200 volts were obtained from a Heathkit Regulated Power Supply, Model P.S. 4; E_f = 6 volts was supplied by 3 storage batteries which were constantly recharged during the operation of the apparatus; RCA 5734 — Mechano–Electronic Transducer — Tube Department, Radio Corporation of America, Harrison, New Jersey; mV = Beckman 10 to 100 millivolt recorder; 10K — Helipot, 10 × 10^3 Ohm (Model C) Helipot Corp., South Pasadena, California (all other resistors were $\frac{1}{2}$ watt carbon resistors, ±10% tolerance).

of the graph paper is found to be 15.6 mg. The constant K is therefore equal to $\frac{4900 \text{ erg}}{15.6 \text{ mg}} = 314 \frac{\text{erg}}{\text{mg}}$. Relative to this constant the weight of the area under the curve from different samples can be expressed.

Preparation of samples for measurement is of great importance. Samples of different cross-sectional areas will result in different areas under the curve which may be wrongly interpreted as being due to differences in texture qualities. A cooked or uncooked bundle of muscle fibers about 4 mm long is dissected from

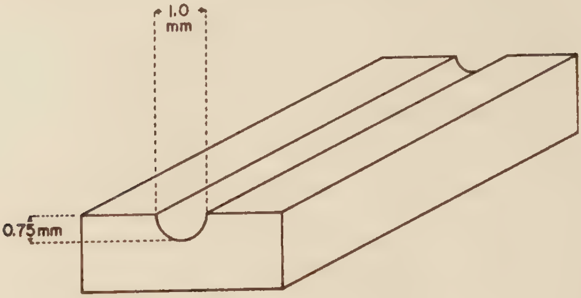

FIG. 3. Brass mold for trimming samples.

between two myocommata and is pressed lengthwise into a brass mold (Fig. 3) which is kept lubricated with glycerol. Applying light pressure with a scalpel, the portions of the muscle fibers protruding above the top surface of the mold are cut off. The sample, which is now flush with the top surface of the mold and is 0.62 mm^2 in cross sectional area, is then pushed out of the mold with a pair of dissecting forceps and is inserted into the horizontal hole of the plunger for measurement. All samples are therefore cut across the fibers.

Cooking of samples was done in a pressure cooker at 15 psi. About 50 g of muscle was placed inside a Petrie dish and cooked for eight minutes. Following the cooking process, any liquid present in the dish was decanted and the sample was left to cool for about one hour before taking measurements.

RESULTS AND DISCUSSION

As can be seen from Fig. 4, the heat denatured samples are always tougher in comparison than the uncooked samples. This is true of beef as well as fish muscle. It was found that the elastic properties of beef fibers disappeared during the cooking process. This did not appear to be always true for the fibers of fish muscle. Although the toughness of mammalian tissue is closely related to its content of connective tissue (Mitchell *et al.*, 1927), in fish muscle the connective tissues dissolve during any cooking process and seem therefore not to influence toughness. Differences in texture between the raw muscle of salmon, lingcod and beef are also noticeable (Fig. 4). Salmon was the most tender of the three samples studied.

Though the deviation in some measurements is very large, the force-distance-diagrams (Fig. 4), can give us additional information concerning the measurement of the work done in cutting a sample. When comparing the peaks obtained for cutting the beef flank cooked for 15 minutes (sample I) and the lingcod frozen during rigor and cooked for 8 minutes (sample H), it is noticed that the baselines for the peaks of sample H are longer, despite the fact that all samples were prepared to equal height (0.75 mm) in the mold. This extension beyond the normal base line of 0.55 cm on the chart can be attributed to greater elastic properties of sample H. This case is further illustrated in comparing paraffin (sample A) and raw beef flank (sample L) which require about the same total

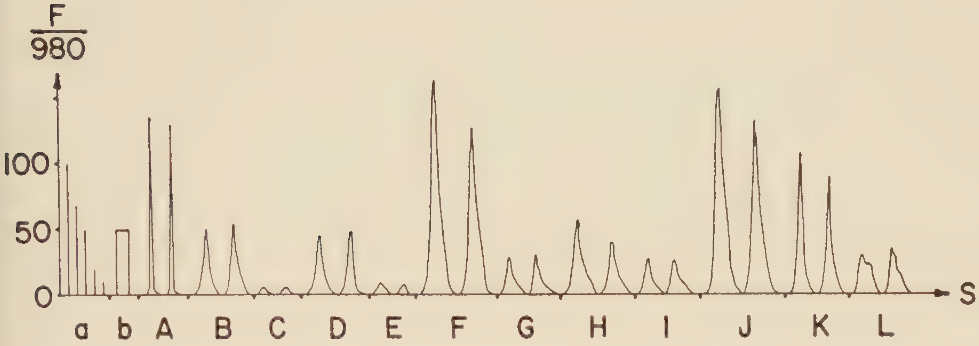

FIG. 4. Two representative force–distance plots of each sample obtained with the fiber shear apparatus.

(a) — Calibration with 100, 70, 50, 20 and 10 gram weights;

(b) — Standard area of 4900 erg (W = Fs).

Sample	Storage temp. (°C) and time	Treatment of sample before test	Work in ergs required to cut average sample	Percentage variation
(A) Paraffin ("Parowax"; Imperial Esso Product)	–		3,670	± 4.5
(B) Salmon (frozen pre-rigor)	– 5 (2 weeks)	cooked (8 min, 15 psi)	4,400	±18.6
(C) Salmon (frozen pre-rigor)	– 5 (2 weeks)	raw	535	± 5.9
(D) Salmon (frozen (pre-rigor)	–30 (2 weeks)	cooked (8 min, 15 psi)	3,300	± 3.3
(E) Salmon (frozen pre-rigor)	–30 (2 weeks)	raw	597	± 5.3
(F) Lingcod (fresh fillets from commercial source)	–30 (4 weeks)	cooked (8 min, 15 psi)	13,500	±12.0
(G) Lingcod (fresh fillets from commercial source)	–30 (4 weeks)	raw	2,390	±16.7
(H) Lingcod (frozen in rigor)	–20 (4 months)	cooked (8 min, 15 psi)	4,590	±23.0
(I) Lingcod (frozen in rigor)	–30 (4 months)	raw	2,510	±15.3
(J) Beef flank (fresh, from commercial source)	–	cooked (11 min, 15 psi)	12,750	±20.2
(K) Beef flank (fresh, from commercial source)		cooked (15 min, 15 psi)	5,680	± 9.9
(L) Beef flank (fresh, from commercial source)		raw	3,450	±20.2

amount of work to be cut. However, the raw beef muscle has very much greater elastic properties than paraffin which increases the base of the peak, i.e. the distance along the abscissa. The paraffin sample, on the other hand, requires a higher maximum force for the cutting process, indicating that it is a very much harder sample. Low variation in cutting the model system of paraffin samples also indicates that considerable variation between the muscle fibers must be expected and is not due to the apparatus.

In comparison to machines developed for measuring shear forces of beef and chicken muscle, the device described in the present paper seems to possess certain advantages. Spencer and Kimbrell (1962) using a standard and a modified Warner-Bratzler shear apparatus reported shear values for model systems which varied between ± 17–32 and ± 13–20%, respectively. Dassau *et al.*, 1962, developed an apparatus for evaluating the texture (shear) of muscle from crab leg, which possesses considerably longer fibers than those of fish muscle.

Whether the shear values obtained with the apparatus described here represent a true measure of texture cannot be stated with certainty until correlation with taste panels has been carried out. Although the energy required to cut a certain sample is very likely to be one dimension of texture, how large a contribution these shear values make to physiologically experienced texture cannot be estimated at this time. It may be, for instance, that elasticity is more related to toughness in stored frozen fish than is shear. Cooking causes marked increases in the shear values. Further experiments to answer some of these questions, and to determine the value of the instrument in assessing increases in toughness of frozen fish stored under different conditions are planned.

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The Bound Nucleotides of Freshly Frozen and Severely Denatured Frozen Lingcod Muscle[1]

By Neil Tomlinson and S. E. Geiger

Fisheries Research Board of Canada
Technological Station, Vancouver 8, B.C.

ABSTRACT

The bound nucleotides of lingcod (*Ophiodon elongatus*) muscle have been examined in relation to the denaturation of muscle proteins during frozen storage. No difference between the quantity of adenine nucleotides (principally adenosine diphosphate) bound in washed muscle residues from freshly frozen (pre-rigor) and in those from muscle severely denatured during frozen storage could be detected. Somewhat more adenosine triphosphate was found bound in crude actin extracts prepared from undenatured frozen muscle than in similar extracts from denatured frozen muscle. Heating lingcod muscle resulted in almost complete release of bound nucleotide.

INTRODUCTION

Dyer and dingle (1961) have reviewed the extensive studies that have been made of the denaturation of fish muscle proteins during the course of frozen storage. This denaturation is of practical importance since it appears to be related to development of "toughness" as measured in the uncooked flesh by the cell fragility method (Love, 1962), and to deterioration in the texture of the cooked flesh (Moorjani *et al.*, 1960), although this latter relationship has not always been observed — deterioration in texture sometimes preceding denaturation of protein in muscle stored at temperatures below –20°C (Van Mameren, 1955; Dyer *et al.*, 1956; Luijpen, 1957). Dyer and Dingle (1961) and Love (1956, 1962) have discussed such deviations, and Love (1962) has suggested that perhaps a small, but not certainly detectable, denaturation of protein actually took place. In any event, the denaturation that does occur has been found to be confined almost exclusively to the actomyosin fraction of the muscle proteins (Dyer and Dingle, 1961). A small loss of "active" actin also occurs (Connell, 1960).

Actin exists in two forms, "G" (globular) and "F" (fibrous). One mole of G-actin has bound to it one mole or somewhat less of adenosine triphosphate (ATP). F-actin is formed from G-actin by polymerization, the process being accompanied by the release of inorganic phosphate from the bound ATP, while the resulting adenosine diphosphate (ADP) remains bound to the protein (Straub and Feuer, 1950; Mommaerts, 1952; Strohman, 1959; Martonosi and Gouvea, 1961; Bárány *et al.*, 1961; also see review by Perry, 1961). G-actin freed from bound nucleotide loses its ability to polymerize (Asakura, 1961; Bárány *et al.*, 1961; Grubhofer and Weber, 1961) but will combine with L-myosin to form nucleotide-free actomyosin. This actomyosin, however, lacks the adenosine

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[1] Received for publication August 3, 1962.

J. Fish. Res. Bd. Canada, 20(1), 1963.
Printed in Canada.

triphosphatase activity of the nucleotide-containing actomyosin formed from G-actin containing bound ATP (Bárány *et al.*, 1961). The actomyosin of muscle contains ADP, apparently bound to the actin moiety (Martonosi *et al.*, 1960). G-actin prepared by depolymerization of F-actin in the presence of free ADP, contains ADP as the bound nucleotide and will polymerize to F-actin without the release of inorganic phosphate but more slowly than G-actin containing bound ATP. (Grubhofer and Weber, 1961). The bound nucleotide of G-actin is thus either essential for certain functions of this protein or protects it from some alteration which may occur in the absence of the nucleotide and which leads to a loss of ability to perform those functions (Bárány *et al.*, 1961; Martonosi and Gouvea, 1961). In muscle, the bound nucleotides appear to be protected from those enzymes which destroy the free adenine nucleotides *post mortem* (Perry, 1952).

Since the bound nucleotides appear to be intimately related to certain functions or to the stability of the proteins that become denatured during the frozen storage of fish muscle, a question arises as to what part they might play in the denaturation process. Saito and Arai (1957) and Jones and Murray (1961a) have examined the changes that occur in the total (free and bound) nucleotides of carp and cod muscle, respectively, during frozen storage at temperatures and for periods of time that would be expected to lead to some denaturation of protein (Dyer and Dingle, 1961). At –5 to –8°C, the adenine nucleotides of carp muscle decreased to apparently relatively stable values at about 60 to 100 days, while in cod ATP fell to a stable value of about 0.26 μmole per g muscle at –14°C in 105 days, following an initial period of 14 days in which it increased from 0.238 μmole at killing (the fish had struggled in the trawl) to 1.53 μmoles. Thus it appears that in cod muscle at –14°C a stable value of ATP was reached while protein denaturation would still be proceeding although near completion (Dyer and Fraser, 1959; Love, 1962). However, while it is possible that the stable values reached represented the bound nucleotides present in the muscle at that time (Jones and Murray, 1961a and b) this has not been definitely established. In addition, it is not known if these stable values would represent the bound nucleotide present when the fish were killed and frozen or if the nucleotides were in fact still bound when the stable values were established.

In the present investigation, the bound nucleotides found in washed residues of freshly frozen and severely denatured frozen lingcod muscle and the bound nucleotides of actin extracts from such muscles have been examined.

METHODS AND MATERIALS

Lingcod were captured by dragging off the mouth of the Fraser River, B.C., and were held in tanks at the Vancouver Public Aquarium. Some of these fish fed in captivity, others did not, but all were used within one or two months of capture.

Unexercised fish were killed by a heavy blow on the head, lateral-dorsal muscle was removed at once, frozen in liquid nitrogen within 2 to 4 min of first disturbing the fish and portions were stored (in polyethylene bags) at temperatures of −30, −20 and −10°C. Samples were removed for examination after various periods of storage as indicated.

Muscle protein soluble in a solution of 5% NaCl in $0.02M$ $NaHCO_3$ (Dyer *et al.*, 1950) or in a KCl-borate solution ($0.025M$ KCl, $0.039M$ borate, pH 7.1) (Perry, 1953) was determined by homogenizing 2.5 g of muscle in about 60 ml of the appropriate solution in a Serval omni-mixer operated at about half maximum speed for 70 seconds, the homogenizer being stopped and restarted at 10-second intervals. The mixer shaft was fitted with a plastic baffle plate to prevent vortex formation and consequent foaming (Dyer *et al.*, 1950). The homogenate was transferred to a stainless steel bottle, the volume was made up to 250 ml with additional extracting solution and the bottle was then placed on a reciprocating shaker (132 one and one-half inch strokes/min). Samples of the homogenate were removed after suitable periods of shaking, centrifuged 15 min at 14,600 × *g* and the protein in solution in the clarified extract was then measured by the biuret method of Snow (1950). Preliminary experiments showed that with undenatured muscle, 1 hour of shaking of NaCl–$NaHCO_3$ homogenates extracted a maximum of protein, little change occurring in this hour. Although air was not excluded from the bottles, only a small decrease in soluble protein was usually observed as the period of shaking was lengthened. With denatured muscle, protein extracted continued to increase during several hours of shaking. For this reason data were recorded for undenatured muscle after 1 hour of shaking, and for denatured muscle after 1 and 24 hours. In extraction with KCl-borate, shaking was continued for 1 hour only. If glass Erlenmeyer flasks were substituted for stainless steel bottles in the shaking procedure quite large decreases in soluble protein occurred during extended shaking periods. All operations were carried out at 0°C, frozen muscle being homogenized without prior thawing. For the purpose of this paper "denaturation" of protein is defined according to Dyer and Dingle (1961), i.e., a change in the protein such that it is no longer soluble or extractable by salt solutions under conditions in which the native protein is soluble or extractable. Total protein nitrogen was measured in muscle from lingcod comparable to those used in the experimental work and was found to be 24.7 mg/g muscle. The fact that there is some variability from fish to fish is shown by the fact that one value as high as 27.3 mg/g for protein nitrogen soluble in 5% NaCl solution has been encountered. However, the data indicate that the method used gives good extraction of protein from undenatured muscle.

The procedure used to wash free nucleotides from muscle in order that the bound nucleotides could be measured was a modification of that used by Perry (1952) for the preparation of myofibrils from mammalian muscle. The muscle sample was homogenized in 100 volumes of KCl-borate buffer (see paragraph above), centrifuged 15 min at 14,600 × *g*, the supernatant solution (after removal of an aliquot for protein determination) was discarded, the residue was resuspended in a second 100 volumes of buffer, again centrifuged and the supernatant solution discarded. The bound nucleotides of the washed residue were extracted for ½ hour with 4% perchloric acid and the denatured protein removed by centrifugation. All steps of the extraction procedure were conducted at 0°C. In contrast with Perry's (1952) findings with homogenates of rabbit muscle, a separate layer of myofibrils did not appear when fish muscle homogenates were centrifuged at 600 × *g* and consequently they could not be separated by this means from other sedimentable material. The high speed centrifugation method adopted was compared with a much more prolonged (10 washings) lower speed centrifugation (600 × *g*) procedure, and was found to give quite comparable results as judged by measurement of ALP (see below) extractable from the washed residues. The clear supernatant solution obtained in the acid extraction was examined by either one of two procedures. In the first, readily acid hydrolyzable phosphate (ALP) in the extract was measured using the method of King (1932) as previously described (Tomlinson *et al.*, 1961), the ultra-violet (UV) absorption spectrum of the extract in the region between 230 and 280 mμ was determined using a Beckman model DU spectrophotometer, and the adenine nucleotide content was estimated using the molecular absorption coefficient of 14.7×10^3 (257 mμ). In the second procedure, the extract was neutralized with cold 4*N* KOH, allowed to stand for 1 hour at 0°C after which the precipitated $KClO_4$ was removed by centrifugation. The clear supernatant solution was then chromatographed on a refrigerated column of Dowex 1 × 8 (Cl^-) by a slight modification of the stepwise elution procedure (using HCl) of Bartlett (1959). The UV absorption of the eluted fractions (15 ml each) was measured at 257 mμ and the adenine nucleotide content of appropriate fractions calculated, again using 14.7×10^3 as the molar extinction coefficient. Nucleotides were identified by their position of elution from the column, their UV absorption spectra, and, when sufficient was present for the purpose, their molar ratio of adenine to ALP to total P. The latter measurements were performed directly on peak fractions from the column, P determinations being carried out as above. Actin was extracted from acetone-dried muscle powder (Bánány *et al.*, 1957) by the procedure of Connell (1960). The extracted actin solution (pH 7.6) was treated with 40 mg of Dowex 1 × 8 (Cl^-) per ml for 5 min at 20°C to remove free nucleotides and inorganic P (Asakura, 1961; Hayashi and Tsuboi, 1960). Sufficient ice-cold 50% perchloric acid was then added to the chilled extract to bring the perchloric acid concentration to 5%. The precipitated protein was removed by centrifugation and the supernatant solution was neutralized with 4*N* KOH, the precipitated $KClO_4$ was removed by centrifugation, and the clarified solution chromatographed as described above, these last steps all being carried out at 0°C.

RESULTS AND DISCUSSION

In Table I the results of examination of acid extracts of washed muscle residues by the first procedure are presented. No loss of bound nucleotide from the muscle during severe denaturation of protein could be detected. The $\frac{250}{260}$ and $\frac{280}{260}$ UV absorption ratios were in reasonable agreement with those expected for a solution of adenine nucleotides, the small deviations observed indicating the presence of a little interference from other UV absorbing material. Examination of three samples by the second procedure showed that in both freshly frozen

(2 samples) and severely denatured (1 sample) muscle, over 90% of the bound nucleotide was accounted for by ADP, in general agreement with the adenine: ALP ratios listed in Table I. Thus in the two freshly frozen samples ADP was found in the amount of 0.38 and 0.36 μM/g; ATP, none detectable and 0.01 μM/g. In the severely denatured sample (stored 1 year at –10°C) ADP amounted to 0.33 μM/g and ATP, 0.015 μM/g. The quantitative differences between these three samples are not considered to be significant, for they fall within the range of differences observed between individual samples in groups with similar storage histories (Table I). The UV absorption spectrum of fractions containing ADP and ATP were in good agreement with those of the pure compounds, as was the adenine: ALP: total P ratio for ADP, e.g., 1:0.97:1.9 (theoretical, 1:1:2) for that from denatured muscle. ATP in all samples was insufficient for accurate measurement of this ratio, and the amount of adenosine monophosphate was too small for accurate quantitative estimation. The fact that nearly all the adenine nucleotides in the washed residues were present as ADP seems to be in accordance with expectations, for the washing procedure would be expected to lead to polymerization of any G-actin present with the consequent conversion of bound ATP to ADP (Moos, 1962). Why such a small proportion

TABLE I. The bound nucleotide and soluble protein of frozen lingcod muscle.

Temperature and duration of storage of sample		Perchloric acid extract of washed muscle residue					Protein N soluble at	
		Adenine[1]	$\frac{\text{O.D. at 250 m}\mu^2}{\text{O.D. at 260 m}\mu}$	$\frac{\text{O.D. at 280 m}\mu^2}{\text{O.D. at 260 m}\mu}$	ALP	$\frac{\text{ALP}}{\text{Adenine}}$	Low ionic[3] strength	High ionic[4,5] strength
		μM/g muscle			*μM/g muscle*		*mg/g muscle*	*mg/g muscle*
–30°C	1 day	.496	.899	.219	.449	.90	6.8	24.3
	1 "	.457	.888	.216	.426	.93	7.0	24.5
	1 mo	.469	.885	.229	.420	.90	5.8	22.2
	1 "	.474	.890	.230	.430	.91	5.5	22.2
	1 "	.470	.902	.218	.430	.91	7.0	21.7
	4 mos	.443	.870	.219	.410	.93	6.5	21.2
–20°C	1 yr 2 mos	.465	.870	.229	.430	.93	3.6	6.6 (10.1)
	1 " 4 "	.441	.840	.226	.440	1.00	5.5	13.7 (17.5)
	1 " 4 "	.431	.870	.240	.397	.92	5.4	8.8 (11.8)
	1 " 4 "	.489	.865	.217	.474	.97	6.7	14.3 (15.7)
	1 " 5 "	.469	.870	.218	.445	.95	6.0	9.6 (11.6)
	1 " 6 "	.469	.870	.204	.445	.95	6.1	15.5 (16.2)
–10°C	1 " 2 "	.508	.866	.232	.484	.95	4.7	6.0 (12.6)
	1 " 2 "	.464	.860	.229	.416	.90	4.9	6.5 (12.6)
	1 " 2 "	.482	.875	.238	.439	.91	5.8	5.8 (9.3)
	1 " 5 "	.491	.856	.221	.487	.99	3.9	6.4 (9.2)
	1 " 6 "	.456	.860	.223	.449	.98	3.3	3.6 (12.7)
	1 " 6 "	.440	.870	.249	.429	.97	3.4	4.1 (6.8)
Averages								
–30°		.468			.427	.91	6.4	22.7
–20°		.461			.439	.95	5.5	11.4 (13.8)
–10°		.473			.451	.95	4.4	5.4 (10.5)

[1] Calculated from the optical density (O.D.) of the acid extracts measured at 257 mμ using 14.7×10^3 as the specific absorption coefficient of adenine nucleotides.

[2] Expected ratios for a solution of adenine nucleotides:

$$\frac{250\ \text{m}\mu}{260\ \text{m}\mu}\ 0.85\ ;\qquad \frac{280\ \text{m}\mu}{260\ \text{m}\mu}\ 0.22\ .$$

[3] Low ionic strength extracting solution was the KCl-borate buffer of Perry (1953).

[4] High ionic strength extracting solution was the NaCl-NaHCO$_3$ solution of Dyer *et al.* (1950).

[5] Bracketed values determined after 24 hours extraction, others after 1 hour (see Methods and Materials).

of the bound nucleotides was accounted for by AMP in the present work in comparison with that found by Jones and Murray (1961b) for leached cod muscle and by Perry (1952) for rabbit myofibrils is not clear, but it is possible that this might be related to differences in method of preparation of the washed extract. There might also be differences between mammalian and fish muscle and between species of fish. The total bound adenine nucleotide found in our work is somewhat higher than that of either the total acid-soluble adenine nucleotides of rested post-rigor or of leached cod muscle, but is of about the same order as that of exhausted post-rigor cod (Jones and Murray, 1961b) and of post-rigor lingcod (Tarr and Leroux, 1962). During the course of frozen storage at −10 and −20°C for the periods of time concerned in the present work, the quantity of total ADP and ATP (free and combined) of pre-rigor frozen muscle would be reduced to a very low value as indicated by determinations of ALP, e.g., values for ALP in lingcod muscle have been found to be reduced from the order of 12–15 μM/g muscle initially to about 1 μM/g during 6 months' storage at −10°C. The rate of reduction is lower at −20°C. (Tomlinson and Jonas, unpublished data). If the assumption is made that the molecular weight of lingcod actin is 62,500, similar to that found for cod actin (Connell, 1958), and if the further assumption be made that the bound ADP and ATP found in lingcod muscle is bound to actin in the ratio of 1 mole adenine nucleotide to 1 mole of actin, it can be calculated that about 11.7% of the dry weight of lingcod muscle is actin, somewhat lower than the value of 15–25% probably contained in cod muscle (Connell, 1960).

Although it appears to be generally accepted that denaturation of fish muscle proteins soluble at low ionic strength (as measured by protein remaining in solution on dilution of an extract made at high ionic strength) does not occur, or is very slight, during frozen storage unless it is accompanied by dehydration of the muscle (Dyer and Dingle, 1961), the present data indicate that there was measurable denaturation of this fraction under our conditions (extraction in KCl-borate buffer). Dehydration of the surface of the stored muscle occurred, but none could be detected by dry-weight determinations of muscle samples used, which were cut from the interior of the pieces stored. The effect of the length of time of shaking the homogenates prior to measurement of the extracted protein on the quantity extracted from denatured muscle seems to indicate that the denaturation measured after 1 hour of shaking is the result in part either of a decrease in ease of extractability (rather than a loss in solubility), or of a denaturation process that is to some extent reversible. The washed residues from the undenatured (−30°C) and from the denatured muscle (−20 and −10°C) were distinctly different from each other. The former were preponderantly gel-like, while the latter were distinctly fibrous. The differences were still observable after acid extraction of the nucleotides, the residues from the denatured muscle being readily dispersed in the acid extracting solution, while those from the undenatured muscle could be only partially dispersed with difficulty.

Data from the investigation of the actin extracts of frozen lingcod muscle are recorded in Table II. The UV absorption spectra of the chromatographic

TABLE II. Nucleotides in crude actin extracts from frozen lingcod muscle.

	Adenine nucleotides (μM/g muscle) and protein N(mg/g muscle) in actin extracts from muscle stored			
	1 mo at −30°C	1 mo at −30°C	11 mos at −10°C	1 yr 6 mos at −10°C
AMP	–	–	–	–
ADP	?	.020	.016	?
ATP	.127	.099	.087	.055
Protein	3.34	5.46	4.19	4.12

Actin extracts were prepared from 20g samples of muscle.

"–" indicates a trace possibly present, but too little for accurate measurement. "?" indicates UV absorbing material present, but absorption spectrum indicated not pure ADP and therefore accurate calculation of quantity not possible. The two values given for ADP should be regarded as maximum values, for in these instances, too, the absorption spectrum was only in fair agreement with that for ADP.

fractions containing ATP were in good agreement with that for the pure compound, as was the adenine: ALP: total P ratio, e.g., 1:2.12:2.96 (theory 1:2:3) for that from a denatured sample. There was somewhat less ATP bound in the extracts from the severely denatured muscle than in those from the undenatured frozen muscle. It should be pointed out that differences that were independent of known variations in preparation have been observed between actin extracts made by procedures very similar to that used in the present work (Weber and Winicur, 1961). However, the results appear to be in agreement with Connell's (1960) findings regarding the slow decrease in "active" actin extractable from cod muscle during the course of frozen storage at -14°C, and, in conjunction with the data for bound ADP and ATP above, lends some further support to the view that changes in myosin are chiefly responsible for the diminishing extractability of actomyosin during frozen storage (Connell, 1960).

A brief investigation was made of the effect of the heating of lingcod muscle on the bound nucleotides. It was found that steaming muscle for 20 min prior to washing it with the low ionic strength KCl-borate buffer resulted in nearly complete disappearance of nucleotide from the washed residue of either freshly frozen or denatured muscle. Similarly, heating washed (KCl-borate solution) muscle residues at 100°C for periods of 4 15 minutes in distilled water (17 volumes of water to 1 part wet weight of muscle) also resulted in the nucleotides being lost from the residues. Some protein was present in solution in the aqueous extract following the heating and clarification by centrifugation, but treatment of such solutions with resin in a similar manner to that used with crude actin extracts resulted in the removal of nucleotide from the extract with negligible loss of soluble protein. It therefore appears that the heating process resulted in release of the bound nucleotide. This is in agreement with an earlier report that heat inactivated actin loses its ability to bind ATP at neutral pH (Drabikowsky, 1961), and with the suggestion of Hamm and Deatherage (1960) that the small increase in soluble non-protein nitrogen that occurs during heating of beef might result in part from the release of bound nucleotides.

Note added in proof:

Since the above was written, a further paper by J. J. Connell has appeared (*J. Sci. Food Agr.*, **13**: 607–617, 1962) in which the changes in the amount of myosin extractable from cod flesh during storage at –14° are described. In his paper Connell presents a very interesting discussion regarding the use of the term "denaturation" in connection with the changes in extractability of the actomyosin fraction in fish muscle.

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An Estimation of the Mortality Rates in a Population of *Tilapia esculenta* Graham (Pisces, Cichlidae) in Lake Victoria, East Africa[1]

By D. J. Garrod[2]

East African Freshwater Fisheries Research Organization
Jinja, Uganda

ABSTRACT

In the commercial fisheries of the great lakes of Central Africa the nylon gill net is the most widespread type of gear in use at present. Recent increases in fishing effort are believed to have had a marked effect upon the abundance of some species and this paper describes a method of estimating the fishing mortality from a fishery of this type. The method is demonstrated in its application to a population of *Tilapia esculenta* in Lake Victoria. In particular the data from the gill net fishery are combined with the known selectivity of the gear to distinguish between fishing mortality and trends in natural loss from the population with increasing age of the fish. The study also shows that the population dynamics of a tropical fish species are amenable to conventional techniques of analysis.

INTRODUCTION

Recent advances in the techniques of analysis of fish populations have enabled workers to develop theoretical models of a fishery from which the effects of changes in fishing pressure on yield and stock abundance may be predicted. In the main these methods have been applied to the great marine fisheries of the northern hemisphere, but it is equally important that similar studies should be carried out on other commercial fisheries of the world to promote rational exploitation of the resource, through fishery management, before unsupervised fishing can damage fish stocks.

This is particularly true on the great lakes of Africa where the fishing is carried out by a multitude of independent fishermen. The increasing demand for protein and cash income from the African populace has in recent years led to a steady increase in fishing effort on lakes close to densely populated areas; and it has been shown, by the analysis of commercial catch statistics (Garrod, 1960), that in some parts of Lake Victoria the fishing effort has risen sufficiently high to cause a reduction in a fisherman's catch per unit effort which is now at marginal low level in some areas. At the same time the total yield from these areas has dropped and it is certain that economic overfishing, and possibly biological overfishing, has occurred.

It is evident that this resource is not at present being exploited to its fullest potential where it will give a sustained yield and at the same time provide individual fishermen with an economic catch per unit effort. The definition of

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[1] Received for publication June 18, 1962.

[2] Author's present address: c/o Fisheries Laboratory, Lowestoft, England.

J. Fish. Res. Bd. Canada, 20(1), 1963.
Printed in Canada.

the level of fishing that will achieve this ideal can rarely be deduced empirically and it is essential that management should be guided by population studies when assessing the degree of fishing to which a fish stock should be subjected.

The determination of these levels requires the formulation of a theoretical model of the fishery based upon a study of the population dynamics of the several commercially important species. The primary step in such an analysis is to estimate the fishing mortality rate that is being caused by a given level of fishing effort, i.e. the proportion of the population killed by fishing in each year.

Such a study was initiated for the fisheries of Lake Victoria as a result of a visit by R. J. H. Beverton of the Fisheries Laboratory, Lowestoft, in 1957, to review the state of the fish stocks which was causing some concern. As a result of his study Beverton formulated a mathematical model of the population of one species, *Tilapia esculenta*, and was able to predict certain effects of fishing upon the stocks of this species and, by analogy, the effects on other species also (Beverton, 1959).

The present paper describes a detailed analysis of the dynamics of a population of *T. esculenta* and defines the relationship between the fishing mortality rate and the amount of fishing for the stock considered. It is appreciated that the concept of rational exploitation should be based upon a combination of similar studies on all representative species within the fishery, but this is not possible at present. This paper, however, describes an approach to the problem which can be applied to any species exploited by a gill net fishery similar to that on Lake Victoria.

METHOD

The general methods by which mortality rates may be estimated are outlined by Beverton and Holt (1956, 1957), Gulland (1955) and Ricker (1958). Basically the determination is a method of expressing the declining abundance of particular age groups as they become progressively older. The total mortality rate (Z) has two components, the natural mortality (M) and, in exploited populations, the fishing mortality (F). Both features are usually given as instantaneous rates which are expressed as exponential coefficients so that, if the abundance of an age group is N at the start of time interval x, then its abundance at the start of the following period $x + 1$ is given by the expression:

$$\mathrm{N}_{x+1} = \mathrm{N}_x \mathrm{S}_x^{t_x} \tag{1}$$

where S represents the survival rate corresponding to the sum of fishing and natural mortality rates during the time interval t_x

$$[\text{i.e. } \mathrm{S}_x^{t_x} = e^{-(\mathrm{F}+\mathrm{M})t_x} \text{ or } e^{-Zt_x}].$$

This expression implies a knowledge of the instantaneous abundance of an age group, but in practice this is not possible and it is customary to base the analysis upon indices of the mean abundance, $\overline{\mathrm{N}}$, of an age group, which Beverton and Holt have shown to be an equivalent measure. Thus:

$$\overline{\mathrm{N}}_x = \frac{\mathrm{N}_x\ (1 - \mathrm{S}_x^{t_x})}{Z_x t_x} \tag{2}$$

using the notation given above.

During a second period t_{x+1} the mean abundance will be:

$$\overline{N}_{x+1} = \frac{\overline{N}_x S_x^{t_x}(1-S_{x+1}^{t_{x+1}})}{Z_{x+1}t_{x+1}} \tag{3}$$

from which:

$$Z_x = \log_e\left[\frac{\overline{N}_x}{\overline{N}_{x+1}}\right] + \log_e\left[\frac{Z_x t_x(1-S_{x+1}^{t_{x+1}})}{Z_{x+1}t_{x+1}\,(1-S_x^{t_x})}\right] \tag{4}$$

If the mortality rates in the two time intervals are not widely different then the second term in (4) can be ignored so that the estimate of total mortality becomes:

$$Z_x = \log_e\left[\frac{\overline{N}_x}{\overline{N}_{x+1}}\right] \tag{5}$$

In most species for which mortality rates have been estimated $t_x = t_{x+1} =$ 1 year, and owing to the selection pattern of the gear, especially trawls, the annual mortality is expected to be constant for all age groups once the fish are fully recruited to the exploited stock. For *T. esculenta* the age determination is based upon spawning rings laid down twice yearly on the scales, so that $t_x = t_{x+1}$ $= 0.5$ year, and all ages in this paper are given as the number of half-years completed. Furthermore, the mortality rates vary between age groups, owing to the selectivity pattern of the gill nets used to exploit the stock.

These nets retain *T. esculenta* over a range of length within which the frequencies of the catches at successive length groups follow an approximately normal distribution about a mean retention length (Holt, 1957; Garrod, 1961). The estimation of the relative abundance of different age groups in a fishery of this type therefore involves a correction for the selective action of the gear: catch records do not give a direct index of abundance as in records of trawl fisheries. For this particular species the procedure is further complicated by the method of ageing fish from the onset of spawning. This does not affect the validity of the mortality estimates when fish are not recruited to the fishable stock until after maturity.

Having established the total mortality rate, it must be subdivided into the two components by the subtraction of the natural mortality rate to give the fishing mortality rate. Tagging experiments have not been successful in this fishery, so that the method of regressing the total mortality coefficient against the fishing effort has been used (Widrig, 1954). In this approach the total mortality coefficient is plotted against the fishing effort for a series of years so that a regression of these data will intersect the ordinate where $F = 0$ at a value corresponding to the natural mortality, assuming that a linear relationship obtains between the fishing effort and the fishing mortality.

In fact, both Widrig (1954) and Paloheimo (1958) have criticised the method owing to its dependence on a good index of the fishing effort, and the possibility of wide fluctuations in the vulnerability of fish from year to year which would cause the regression to be non-linear. Paloheimo has overcome this by assessing the abundance of an age group from the 'virtual population' (the total contribution of an age group to the fishery in subsequent years), correcting this for the varying amount of fishing in each year. The mortality estimates are then derived from these estimates of abundance. This method requires data from a considerable number of years and cannot be applied in the present study. However, for *T. esculenta* the methods of fishing are very uniform and the exploited stock occupies a restricted habitat, so that there is no reason to suppose that Paloheimo's and Widrig's criticism of the regression method will obtain.

In this study, therefore, the method of Widrig (1954) has been used and extended to give an estimate of the natural mortality of each age group from a knowledge of the differential selectivity of the fishing gear. The value of this extension has been appreciated and discussed (Beverton and Holt, 1956), but it has not been widely used in practice.

SAMPLING PROCEDURE

Gulland (1955, 1957) has discussed the general theory of fish sampling. Owing to the vast area of Lake Victoria it has not been possible to study each important *T. esculenta* stock and the determinations described in the following study apply only to the North Buvuma Island stock. This population is centred upon the shallow bays to the north of the Island which are sheltered from the prevailing southeasterly winds. The area of the habitat is difficult to estimate owing to the nature of the shoreline, but it is given as approximately 50 square miles (130 km^2). The region is isolated from other *T. esculenta* habitats by deep water in the Dagusi Island area to the southeast, and by the Buvuma Channel to the northwest. It is particularly convenient because almost all the fish taken from the area are landed at an intermediate landing, Waigalla. This has no access road and all the fish must be ferried to the central market after having been removed from the nets. This process gives a field worker sufficient time to collect adequate data without seriously inconveniencing the fishermen.

(a) African Fishing Methods

The fish catches from the unit stock of *T. esculenta* are landed daily at sunrise at Waigalla, some 15 miles (24 km) from Jinja. Fishing is carried out by a variable number of Africans of three tribes, Basoga, Baganda and Jaluo, all of whom use the same gear, 4½-inch (114-mm) nylon gill nets, weighted to fish on the bottom. This and all subsequent mesh measurements are taken between alternate knots when the net is stretched. The technique of dealing with fish catches differs between tribes in that the Basoga and Baganda remove fish from the nets as soon as they are lifted on to the canoes, whereas the Jaluo lift the nets with the fish still enmeshed and then bring the nets ashore for sorting before the fish are removed. This is of importance because fish catches of the Basoga and Baganda are ready for ferrying to the central market as soon as the fishermen return, so that the opportunities to measure their catches are few compared to the ease of sampling the catches of Jaluo fishermen whose fish remain on the beach for some time while sorting takes place.

(b) ESTIMATION OF TOTAL FISHING EFFORT AND TOTAL YIELD FROM THE AREA

The great marine commercial fisheries of temperate climates are exploited by a variety of gears and vessels so that the choice of a valid unit of effort is a complex determination (Beverton and Holt, 1957; Parrish and Keir, 1959). With the African *T. esculenta* gill net fisheries the position is less complicated because of the localisation of the stocks and the uniformity of the gear and vessels used, so that an enumeration of the total catch and the number of nets used provides sufficient basic information.

At Waigalla landings take place over approximately 200 yards (180 m) of shoreline only, so that it is not difficult to assess the composition of all catches landed. An African fishguard was employed to carry out a total enumeration of all fish landed by each canoe together with the number of nets used. This man also kept a record of fishermen's movements, changes in fleet composition, etc.

For each month a diary of each canoe was maintained so that an entry could be made according to whether or not a canoe fished, and if so the number of nets used. On some days the fishguard was unavoidably absent but the number of nets used could be entered with a high degree of accuracy from the figures for the day before and after. A complete estimate of fishing effort was obtained in this way but it was not possible to estimate fishing intensity in any one sub-area because of the inherent reticence of fishermen on such matters.

The fishing effort has been expressed as the number of gill net nights, nets being fished from sunset to sunrise. This is the most accurate measure of effort, the 'canoe night' unit being unsatisfactory owing to the wide variation in the number of nets used.

Even so the gill net as a unit of effort is subject to error for two reasons: (*i*) Fishermen will use a net without any maintenance so that eventually it is little more than a head and footrope with an efficiency only a fraction of that of a new net. As the 'rains' begin and fishermen expect increased catches, the proportion of new nets increases. It was impossible to maintain a check on this owing to the methods of dealing with the catches, and it has been necessary to assume that the rate of replacement of old nets by new nets was constant, i.e. that the efficiency of all nets was the same. (*ii*) The variation in lengths of the gill net 'gangs' or fleets influences their efficiency, either because it requires a longer period of time to set and lift 100 nets than 30, or because longer fleets of nets extend over more varied fishing grounds. This variation in efficiency is reflected in the catch per net data from fleets of differing lengths, which are illustrated in Fig. 1. There is a decline in the catch per net with increasing fleet length.

The effect upon total catch records of either source of error has been impossible to estimate, but they are probably not significant because in final calculations the fishing effort has been averaged over 6 monthly periods, each period including a 'rainy' season.

The total count records thus give an estimate of fishing effort and, in a similar way, the total number of fish of each species landed.

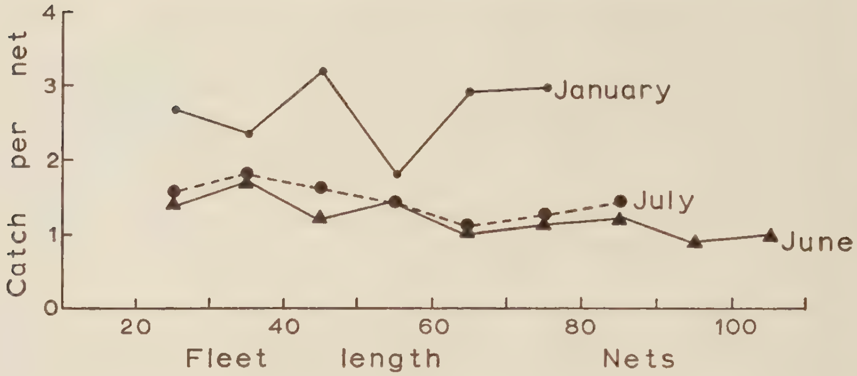

FIG. 1. The variation of catch per net with increasing numbers of nets per gang (fleet).

(c) ESTIMATION OF THE LENGTH FREQUENCY DISTRIBUTION OF COMMERCIAL CATCHES

Detailed catch sampling was carried out by myself and two colleagues, and later an African assistant. The landing was visited twice weekly, arriving at the same time as canoes began landing. If possible, visits were made on the same days in each week because regular routine is an asset in coöperating with staff and fishermen. Random variation is likely to cause complete disorganization and where, as in this study, fishermen are operating in the same region each day, there is no advantage in avoiding systematic visits.

These visits were carried out for two years, October 1958 to October 1960. During each visit a number of catches were analysed and a detailed length frequency record taken of all *T. esculenta* caught. The size of individual canoe catches rarely exceeded 100 fish so that sub-sampling was unnecessary. The total length records were pricked through polythene on to a calibrated printed form mounted on a cork faced measuring board.

When a canoe had been selected for recording, fish were taken as rapidly as possible and their total length pricked on to the record sheet. Any one fish would be given to the assistant who removed at least 3 scales from its flank whilst length frequency recording was continued. The scales were placed in an envelope in a box arranged according to the length groups being sampled. When the assistant had completed this classification he was handed another fish for scale sampling, irrespective of its length. In this way the sampling for age was randomised without bias owing to the overlap of length for age in *T. esculenta*, and the similarity in appearance of old and young fish of the same length. At the beginning of this study the Research Organization undertook the ferrying of fish for fishermen and sampling took place on the return trip. This procedure introduced bias into the catch sampling because only certain canoe owners were sufficiently coöperative to allow us to handle their fish. Because of this it became necessary to measure fish on the beach, selecting canoe catches to be measured as they came ashore. This procedure is also biased as canoes with better catches of *T. esculenta* were preferred, giving overestimates of the catch per unit effort. However, the percentage length frequency of these distributions are valid and have been adjusted to give the true length frequency distribution by using the catch per net obtained from total count records. This is in any case more valid because it required considerable interrogation in tribal vernacular to determine the number of nets used, and this was best left to the African fishguard. An analysis of the variance of data taken during July 1960, one of the months during which sampling was least adequate, gave a variance ratio (F) of 0.031 where $n_1 = 3$, $n_2 = 863$, illustrating the homogeneity of the data.

All fish were measured to the nearest centimetre below for total length and 0.5 cm added to each value following the calculation of average length.

No routine mesh measurements of commercial gear were maintained but a check was kept by interrogation of the net retailers. A second check was obtained by recording the length frequency distribution of *Tilapia variabilis* which were also caught, as a biological indicator of changes in mesh size. Gill net meshes are extremely selective for length of *Tilapia* species and any change in mesh size is reflected by a change in the average size of fish caught. Table I shows that

TABLE I. Quantities of fish and canoes landing at Waigalla, October 1958 to October 1960; also their average length and their standard deviation in length (S.D.).

	Canoes			No. of fish		Length of fish	
Month	Landed	Sampled	Sampled	Landed	Measured	Mean	S.D
1958	*no.*	*no.*	%	*no.*	*no.*	*mm*	*mm*
October	722	28	3.9	69,500	2657	293	5.1
November	500	60	12.0	30,000	4058	297	5.7
December	481	35	7.3	45,000	4468	299	2.8
1959							
January	1005	38	3.8	99,000	4912	299	2.6
February	1092	34	3.1	89,000	3724	298	4.9
March	784	36	4.6	75,000	3697	297	1.0
April	1011	41	4.1	65,000	3889	294	6.5
May	906	42	4.6	62,000	4206	288	5.4
June	389	48	12.3	10,000	2058	288	6.3
July	341	40	11.7	11,000	2040	285	5.0
August	320	25	7.8	10,000	1562	287	5.8
September	383	29	7.6	22,500	1995	291	4.9
October	375	30	8.0	29,000	3366	294	6.5
November	272	21	7.7	25,000	2979	290	5.4
December	258	24	9.3	22,000	3277	292	6.2
1960							
January	259	25	9.7	16,500	2126	296	5.2
February	271	19	7.0	19,000	1923	293	4.0
March	334	28	8.4	42,000	3200	294	4.2
April	539	25	4.6	54,500	2205	292	4.2
May	463	29	6.3	25,000	1797	291	5.0
June	217	13	6.0	3,000	328	289	5.6
July	390	24	6.2	7,500	867	284	9.2
August	498	16	3.2	30,500	865	286	7.3
September	754	29	3.8	37,000	2084	289	9.9
October	761	20	2.6	50,000	2669	284	8.1

there was a systematic change in the average length of *T. esculenta* catches. This decrease was caused by a decline in the abundance of larger fish and increased numbers of new recruits at the lower end of the 4½-inch gill net selection range. It is not caused by changing morphometry of the fish nor is it caused by a change in the mesh size of commercial gill nets, because there was no comparable decrease in the average lengths of *T. variabilis* caught during the same months (Fig. 2).

The scale collections were examined each month. Three scales from the flank of each fish were examined under a low power microscope, the scales being mounted in a film of water. A previous study (Garrod, 1959) has shown that the scales of *T. esculenta* bear a series of rings which may be used as age indicators and in this work the rings were counted, a particular note being made as to whether or not a ring was being laid down on the edge of the scale. In each month scales from 50 fish in each centimetre length group were examined.

The data on which this analysis is based are thus a total count of fish landed and fishing effort (gill net nights) in the Waigalla area, together with length frequency distribution of the commercial catch reduced to the percentage composition per centimetre length group, and detailed monthly age distribution samples of each centimetre length group.

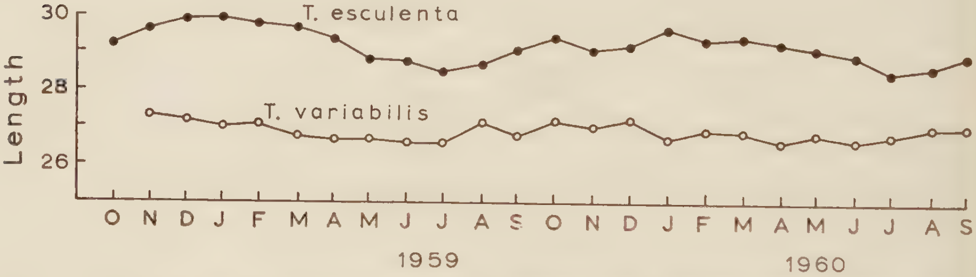

FIG. 2. The variations of the mean lengths of *T. esculenta* and *T. variabilis* taken in commercial gill nets.

RESULTS AND ANALYSIS

(1) CALCULATION OF THE TRUE RELATIVE ABUNDANCE OF EACH LENGTH GROUP

The interpretation of age of *T. esculenta* is based upon the formation of two rings on the scales in each year to coincide with the rainy seasons, which are clearly separated by the June, July, and August cool season and the January, February dry season. The age data are therefore divided into 6-month periods, January June and July December, and the treatment of length frequency data has been similarly divided.

An example of the treatment of these data for the period January–June 1959 is given in Tables II-A to II-D. The catch per net per month obtained from the total count records is subdivided according to the percentage length frequency distribution from the catch sampling (Table II-A), to give an accurate catch per net per month per length group (Table II-B).

TABLE II-A. Proportional abundance of length groups in length frequency distributions, January–June 1959. (The percentages do not total 100 for each month owing to the exclusion of some length groups from the table.)

	Midpoint of length group, *cm*								Catch per net
	26.5	27.5	28.5	29.5	30.5	31.5	32.5	33.5+	
	%	%	%	%	%	%	%	%	*no.*
Jan.	2.2	8.4	18.1	25.9	21.5	14.2	5.5	3.4	1.850
Feb.	3.1	11.7	20.5	25.2	19.6	11.4	4.5	3.3	1.590
Mar.	3.5	11.0	20.5	23.4	22.0	11.1	4.5	3.2	1.530
Apr.	8.3	15.6	20.6	19.4	16.0	9.8	4.4	3.0	1.330
May	13.1	18.5	21.0	18.8	12.2	6.2	2.4	2.0	1.310
June	11.4	20.1	21.8	18.3	12.7	6.8	2.3	2.9	0.460

TABLE II-B. Actual catch per 1000 nets of each length group, January–June, 1959.

	Midpoint of length group, *cm*							
	26.5	27.5	28.5	29.5	30.5	31.5	32.5	33.5+
Jan.	41	155	335	479	398	263	102	54
Feb.	49	186	326	401	312	181	72	48
Mar.	53	168	314	358	337	170	69	47
Apr.	110	207	274	258	213	130	59	44
May	172	242	275	246	160	81	31	26
June	52	92	100	84	58	31	11	16

TABLE II-C. Selectivity of 4½-inch gill net. (Mean retention length = MRL = 29.2 *cm*; standard deviation = σ = 1.48.)

	Midpoint of length group, *cm*								MRL
	26.5	27.5	28.5	29.5	30.5	31.5	32.5	33.5+	29.2
Distance from MRL	2.7	1.7	0.7	0.3	1.3	2.3	3.3	4.3	0
Distance/σ	1.82	1.15	0.47	0.20	0.88	1.55	2.23	2.91	...
Ordinate of normal distribution	.0761	.2059	.3572	.3910	.2709	.1200	.0332	.0058	.3989
Percentage of 0.3989	19.08	51.62	89.55	98.02	67.91	30.08	8.32	1.45	100.
Adjustment	19.08	51.62	89.55	98.02	82.60	46.90	25.50	10.20	...

TABLE II-D. True relative abundance of the length groups: i.e., (catch per net)/(percentage adjustment).

	Midpoint of length group, *cm*							
	26.5	27.5	28.5	29.5	30.5	31.5	32.5	33.5+
Jan.	.215	.300	.374	.489	.482	.561	.400	.534
Feb.	.257	.360	.364	.409	.378	.386	.282	.475
Mar.	.278	.325	.351	.365	.408	.362	.271	.465
Apr.	.577	.401	.306	.263	.258	.277	.231	.436
May	.901	.469	.307	.251	.193	.173	.122	.259
June	.273	.178	.112	.086	.070	.066	.043	.161

The retention curve of $4\frac{1}{2}$-inch mesh nylon nets has been previously determined (Garrod, 1961); it is an approximately normal curve with a mean retention length 29.2 cm and a standard deviation of 1.48 cm. A correction factor may then be applied to the catch per net index for each length to give an index of true abundance relative to that of fish caught at the mode of the net where its efficiency is maximum. This correction has been applied to each length for each month and then this corrected abundance was averaged over 6-month periods to give an average abundance of fish of each length group which is directly comparable with the abundance of the adjacent length groups.

In practice it was found that at lengths considerably greater than the mean retention length the correction gave astronomical indices of abundance. This illustrates a typical feature of gill net length frequency distributions, that greater numbers of fish are caught at the upper limit of the selection range than would be predicted from theory, as the theoretical curve underestimates the efficiency of the net at these lengths. For lengths exceeding 30.5 cm the theoretical correction factor has been slightly modified by a factor taken from the actual relative abundance of the larger fish during this study. This is valid because at the lengths in question the abundance of single centimetre groups remained relatively unchanged. The figures given in Table II-C have been corrected in this way.

It will be noted that fish of less than 26.0 cm are rare in the commercial catches and in all further calculations *T. esculenta* is considered to be recruited to the exploited stock at 26.0 cm, and not captured at all at smaller sizes.

The average abundance of each length group in each 6-month period, as calculated in Table II-D, is given in Table III, using the catch per unit effort as an index of abundance.

TABLE III. True relative abundance of length groups (in terms of catch per net), by half-years. In this and succeeding tables the January–June and July–December periods are abbreviated as (1) and (2) respectively.

	Midpoint of length group, *cm*							
	26.5	27.5	28.5	29.5	30.5	31.5	32.5	33.5+
1958(2)	0.28	0.33	0.39	0.47	0.44	0.40	0.28	0.38
1959(1)	0.42	0.34	0.30	0.31	0.30	0.30	0.22	0.39
1959(2)	0.67	0.41	0.26	0.22	0.20	0.21	0.18	0.23
1960(1)	0.65	0.44	0.28	0.23	0.23	0.31	0.32	0.45
1960(2)	1.18	0.65	0.32	0.19	0.18	0.20	0.20	0.22

(2) ESTIMATION OF THE PERCENTAGE AGE COMPOSITION OF EACH LENGTH GROUP

From the hypothesis of two rings being laid down during each year to coincide with successive rainy periods the year is divided into two 6-month periods so that the fish of a given age during one 6-month period will be one ring older in the following period. Fish with no rings are believed to be fish recruited to the fishable stock which are about to lay down a ring, and fish which are in the process of laying down a ring on the edge of the scale are included in the 0 ring group. Fish become "1-ringers" and enter their second season on the completion of this ring and the renewal of scale growth which attends it. Similarly fish in the 2-ring group are those that have completed the second ring and show renewed scale growth and may even show an incomplete third ring on the edge of the scale, but do not enter the three ring group until this ring is complete.

The scale samples were collected according to the length group and on analysis were divided to give the number of fish in the sample that fell into each ring group. The samples for each month during the 6-month periods were then summed to give one large sample for the period for each length group. An example of this is given in Table IV. There was no distinction between sexes.

TABLE IV. A typical six-month scale sample, January–June, 1959, for 29.0–29.9 cm length group.

	Number of fish in each ring group							
Ring group	Jan.	Feb.	Mar.	Apr.	May	June	Total	Percentage
0	2	1	1	2	10	3	19	3.9
1	6	4	3	1	6	1	21	4.3
2	9	3	1	7	7	6	33	6.7
3	22	14	21	9	9	5	80	16.3
4	24	12	25	23	15	16	115	23.4
5	19	21	12	20	10	8	90	18.3
6	11	7	20	12	10	9	69	14.0
7	4	4	4	7	13	5	37	7.5
8	2	2	3	1	4	4	16	3.3
9	2	—	1	1	2	—	6	1.3
10	—	—	—	—	1	4	5	1.0
11+	—	—	—	—	—	1	1	0.3
Discarded	6	1	2	4	1	4	18	...
Total							492	

Approximately 5% of the scales were discarded either because of erosion obscuring the rings, or unreliability of the interpretation; these were assumed to be divided in the same proportion as shown by other fish of the same length group. The range of age for a given length should be particularly noted.

The percentage age (ring) compositions of each length group for each period are given in Table V. These percentage frequency distributions for each length cannot be used to estimate growth because the representation of higher age groups within a length group has been influenced by the effects of fishing and would thus bias such an estimate. The growth rate must be separately determined.

(3) ESTIMATION OF INDICES OF THE TRUE RELATIVE ABUNDANCE OF EACH AGE GROUP

This estimate is obtained by the combination of (1) and (2) above. The catch per net of each length group (Table III) is subdivided according to the percentage contribution of each ring group (Table V), thus giving an estimate of

TABLE V. Percentage age composition of each length group, by half years.

	Midpoint of length group—*cm*							
Age	26.5	27.5	28.5	29.5	30.5	31.5	32.5	33.5+
A. 1958(2)								
0	28.1	10.9	1.9	0.5				
1	21.6	15.1	10.7	3.4	1.5	0.5		
2	15.1	21.9	12.6	15.4	8.2	2.5	1.6	0.5
3	12.9	16.7	27.7	24.0	20.4	17.7	11.0	1.6
4	10.1	18.7	26.7	27.9	27.6	24.1	19.4	12.0
5	8.6	9.4	12.1	15.9	15.8	13.3	13.6	8.2
6	2.2	5.2	2.9	9.1	13.8	20.2	17.3	16.4
7	0.7	1.0	4.2	2.4	5.6	10.3	14.1	9.8
8	0.7	1.0	0.9	1.4	5.1	7.4	14.7	20.8
9	...	...	...	...	2.0	3.0	5.2	13.7
10	...	...	...	...	...	1.0	2.6	12.4
11+	...	...	...	...	...	...	0.5	4.4
Sample size	139	192	206	208	196	203	191	183
B. 1959(1)								
0	35.2	19.3	10.6	3.9	0.6			
1	25.2	19.8	9.2	4.3	0.6	0.4		
2	13.2	16.9	12.8	6.7	4.6	3.4	1.1	
3	8.8	15.6	18.1	16.3	14.7	6.0	5.4	1.6
4	8.2	13.7	18.8	23.4	23.6	17.6	13.4	4.0
5	6.7	6.6	14.4	18.3	18.5	18.0	18.3	7.1
6	1.2	3.9	7.6	14.0	19.0	18.7	16.3	10.3
7	1.2	2.2	3.9	7.5	6.9	15.5	13.6	18.3
8	...	1.5	3.9	3.3	5.8	10.9	13.4	18.0
9	...	0.2	0.5	1.3	3.2	4.7	8.9	19.6
10	...	0.2	...	1.0	1.8	3.4	7.1	13.5
11+	...	...	0.2	0.3	0.6	1.3	2.5	7.7
Sample size	357	409	436	492	496	466	448	378
C. 1959(2)								
0	20.9	10.9	4.5	1.1	0.3			
1	43.3	31.2	20.0	7.0	1.4	0.4		
2	15.6	18.9	13.5	9.6	5.2	2.6	0.4	
3	6.0	13.0	13.5	13.8	10.8	6.0	1.7	1.9
4	5.7	7.0	17.1	21.3	17.8	15.7	10.7	5.0
5	2.7	8.1	12.9	17.7	26.5	26.0	23.6	16.8
6	3.4	4.9	8.7	15.2	11.5	18.7	18.0	16.8
7	0.8	3.2	5.2	5.9	15.0	14.0	16.3	18.6
8	...	1.8	2.9	3.7	5.9	7.7	10.3	13.7
9	1.1	0.7	1.0	2.5	3.8	5.5	8.6	8.7
10	...	...	0.6	1.1	1.0	2.1	7.3	14.3
11+	...	...	...	1.1	0.7	1.3	3.0	4.3
Sample size	263	285	310	356	287	236	233	161
D. 1960(1)								
0	19.7	11.9	21.2	1.7	0.4			
1	41.5	36.2	21.2	10.0	2.0			
2	23.8	27.1	15.9	13.6	4.7	1.9	1.3	1.7
3	10.9	8.7	10.1	10.7	12.2	6.8	2.6	1.7
4	2.1	8.3	17.8	19.0	24.8	13.0	10.5	10.2
5	1.0	3.7	8.2	15.3	18.9	26.5	24.2	25.4
6	0.5	2.8	2.9	13.2	19.3	17.9	21.6	18.6
7	0.5	1.4	1.4	7.9	8.3	13.6	17.6	14.4
8	...	...	1.0	4.1	3.9	9.3	9.8	8.5
9	...	...	...	3.8	1.2	6.2	6.3	10.2
10	...	...	...	...	3.6	2.5	5.2	5.1
11+	...	...	0.5	0.8	0.8	2.5	0.7	4.2
Sample size	193	218	208	242	254	162	153	118

TABLE V. Percentage age composition of each length group, by half years. (Cont'd)

	Midpoint of length group—*cm*							
Age	26.5	27.5	28.5	29.5	30.5	31.5	32.5	33.5+
E. 1960(2)								
0	11.8	14.1	8.6	3.1				
1	26.0	21.5	23.0	10.8	2.2			
2	28.0	36.1	21.3	15.4	3.4	3.4	0.1	
3	18.6	15.2	23.6	17.9	6.2	3.4	0.1	
4	5.0	7.9	10.3	13.8	11.8	7.6	5.8	5.7
5	...	1.0	5.2	12.3	16.9	11.9	16.3	14.3
6	...	1.5	3.4	11.8	18.5	22.9	18.6	20.0
7	0.6	2.1	4.0	7.7	13.5	15.3	19.8	14.3
8	...	0.5	0.6	4.1	10.7	16.9	10.5	14.3
9	...	...	...	2.0	5.1	11.0	12.8	14.3
10	...	...	...	0.5	10.1	5.9	10.5	14.3
11+	...	...	...	0.5	1.7	1.7	3.5	2.9
Sample size	161	191	174	195	178	118	86	35

the true abundance of each group in the population exceeding 26 cm in length (Table VI). These do not represent the absolute total abundance of the ring groups because a proportion of the population of 0, 1, 2, 3, and 4 ring fish has not been recruited to the exploited population, i.e. they are less than 26 cm.

The indices of abundance of each ring group given in Table VI are illustrated in Fig. 3. The main point of interest in this figure is the consistency of abundance of groups exceeding 5 rings throughout the period of this study. The extreme variability of the abundance of earlier ring groups reflects the variation of recruit abundance from season to season. The average abundance of each ring group is indicated to show that recruitment to the exploited stock is not complete until fish are at least 4 rings old, i.e. have been in the fishable stock for two years. For all other purposes the average has no meaning.

TABLE VI. Indices of the true abundance of each age group. (In terms of 1000 × catch per net).

	Midpoint of length group—*cm*								
Age	26.5	27.5	28.5	29.5	30.5	31.5	32.5	33.5+	Total
A. 1958(2)									
0	078	037	007	002	...	...	...	...	124
1	060	051	042	016	007	002	...	...	178
2	042	073	049	072	036	010	004	001	287
3	036	056	108	113	077	072	030	005	497
4	028	063	104	131	121	098	054	034	633
5	024	031	047	075	069	054	038	035	373
6	006	017	011	043	060	082	048	053	320
7	002	003	016	011	024	042	039	044	181
8	002	003	004	007	022	030	041	067	176
9	...	...	...	...	009	012	014	050	095
10	...	...	...	...	...	004	007	048	059
11+	...	...	...	...	...	...	001	031	032

TABLE VI. Indices of the true abundance of each age group. (In terms of 1000 × catch per net). (Cont'd)

Age	Midpoint of length group—*cm*								
	26.5	27.5	28.5	29.5	30.5	31.5	32.5	33.5+	Total
B. 1959(1)									
0	148	066	032	012	002	. . .	. . .	. . .	260
1	107	067	028	013	002	001	. . .	. . .	218
2	055	057	038	021	014	010	002	. . .	197
3	037	053	054	051	044	018	012	004	273
4	034	047	056	073	071	053	029	012	375
5	028	022	043	057	056	054	040	023	323
6	005	013	023	043	057	056	036	036	269
7	005	007	012	023	021	046	030	061	205
8	. . .	005	012	010	017	033	029	071	177
9	. . .	001	002	004	010	014	020	074	125
10	. . .	001	. . .	003	005	010	016	060	095
11+	. . .	. . .	001	001	002	004	006	047	062
C. 1959(2)									
0	140	045	012	002	001	. . .	. . .	. . .	200
1	290	128	052	015	003	001	. . .	. . .	489
2	104	077	035	021	010	005	001	. . .	253
3	040	053	035	030	022	013	003	004	200
4	038	029	044	047	036	033	019	011	257
5	018	033	034	039	053	055	042	039	313
6	023	020	023	023	023	039	032	039	222
7	005	013	014	013	030	029	029	043	176
8	. . .	007	008	008	018	016	019	031	107
9	. . .	003	003	006	008	012	015	020	067
10	. . .	. . .	002	002	002	004	013	033	056
11+	. . .	. . .	. . .	002	001	003	005	010	021
D. 1960(1)									
0	128	052	059	004	001	. . .	. . .	. . .	244
1	270	159	059	023	005	. . .	. . .	. . .	516
2	155	119	045	031	011	006	004	006	377
3	071	038	028	025	028	021	008	008	227
4	014	037	050	044	057	040	034	044	320
5	006	016	023	035	043	082	077	113	389
6	003	012	008	030	044	055	069	083	304
7	003	006	004	018	019	042	056	065	213
8	. . .	. . .	003	009	009	029	031	035	119
9	. . .	. . .	. . .	009	003	019	020	046	097
10	. . .	. . .	. . .	. . .	008	008	017	023	056
11+	. . .	. . .	. . .	002	002	008	002	020	034
E. 1960(2)									
0	139	092	027	006	. . .	. . .	. . .	. . .	264
1	306	140	073	021	004	. . .	. . .	. . .	544
2	330	234	068	030	006	007	. . .	. . .	675
3	219	099	075	034	011	007	. . .	. . .	445
4	059	051	033	026	021	015	012	012	229
5	. . .	006	016	024	031	024	033	031	165
6	. . .	010	011	023	034	046	038	043	205
7	007	014	013	015	025	031	040	031	176
8	. . .	003	002	008	019	034	021	031	118
9	. . .	. . .	. . .	004	009	022	026	031	92
10	. . .	. . .	. . .	001	018	012	021	031	83
11+	. . .	. . .	. . .	001	003	003	007	007	21

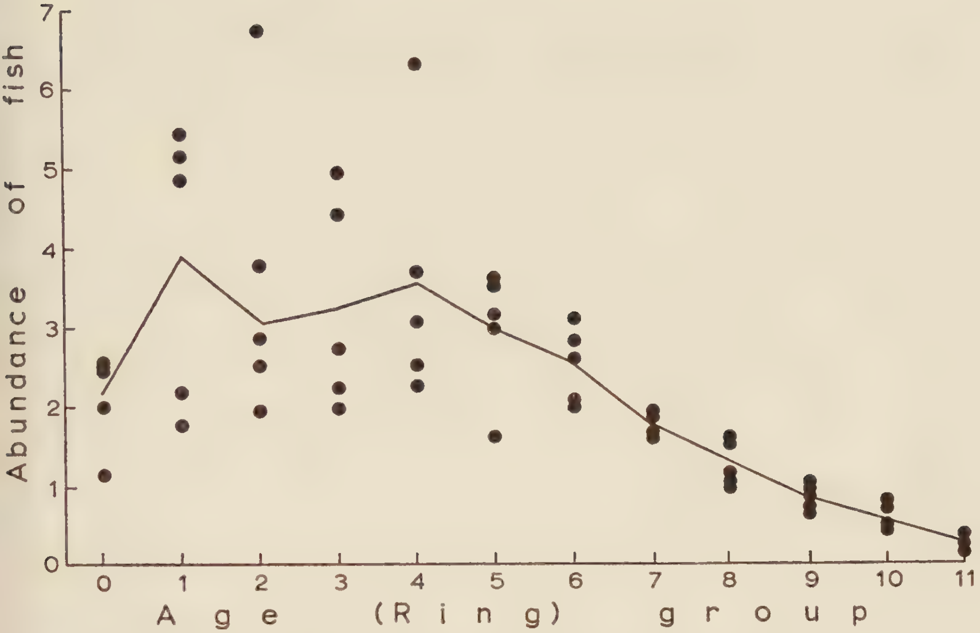

FIG. 3. The average abundance of different age groups. Data from Table VI.

(4) THE BROAD IMPLICATION OF THE VARIED ABUNDANCE OF DIFFERENT AGE GROUPS

It has been shown in (2) above that the abundance of fish of one season's recruitment should be followed throughout its growth through the exploited stock to determine the true effects of fishing. This means that fish having 1 ring in the October/December 1958 season are the same fish that show 2 rings in the January/June 1959 season, and 3 rings in the July/December 1959 season and so on. This principle can be applied to each ring group which itself can be referred to the season when it entered the fishable stock, depending on the number of rings shown at the beginning of this study. For example, fish with 3 rings at the beginning of this study, i.e. in their 4th season, must have entered the fishable stock in the first half of 1957. The totals for each ring group, shown in Table VI, are arranged according to the abundance of each spawning group in Table VII-A, but owing to the duration of this study, it is only possible to follow any one group through 5 seasons. To obtain the abundance of single-season spawning groups the Table is read horizontally, while the actual abundance of one ring group in any one of the seasons during this study is given by reading diagonally down.

The abundance of the spawning groups which were all represented in the first half of 1959, i.e. excluding fish entering the fishable stock in July–December, 1959 and in 1960, has been illustrated by Fig. 4. It is clear that in a unit stock such as this the abundance of spawning groups will change systematically during their growth through the exploited phase, so that it is possible to approximate the variation for any one spawning group by a line fitted by eye. This involves a substantial alteration of only 4 estimates of abundance of the total 45. These are "4-ringers" in the January/June 1958 group, "5-ringers" in the July/December 1957 group, "3-ringers" in the January/June 1957 group and "4-ringers" in the July/December 1957 group. The estimates of abundance have been corrected to the trends shown in Fig. 4 and are given in Table VII-B.

TABLE VII-A. Abundance of single spawning groups in successive seasons, arranged by season of entry to the fishable stock. (Unit as in Table VI)

Season of entry	Ring group											
	0	1	2	3	4	5	6	7	8	9	10	11
1960(2)	264											
1960(1)	244	544										
1959(2)	200	516	675									
1959(1)	260	489	377	445								
1958(2)	124	218	253	227	229							
1958(1)	...	178	197	200	320	165						
1957(2)	...	...	287	273	257	389	205					
1957(1)	...	...	...	497	375	313	304	176				
1956(2)	...	...	...	...	633	323	222	213	118			
1956(1)	...	...	...	...	...	373	269	176	119	092		
1955(2)	...	...	...	...	...	...	320	205	107	097	083	
1955(1)	...	...	...	...	...	...	...	181	177	067	056	021
1954(2)	...	...	...	...	...	...	...	...	176	125	056	034
1954(1)	...	...	...	...	...	...	...	...	...	095	095	021
1953(2)	...	...	...	...	...	...	...	...	...	...	059	062
1953(1)	...	...	...	...	...	...	...	...	...	...	...	032

TABLE VII-B. Corrected estimates of abundance of single spawning groups in successive seasons, arranged by season of entry to the fishable stock. (Unit as in Table VI).

Season of entry	Ring group											
	0	1	2	3	4	5	6	7	8	9	10	11
1960(2)	264											
1960(1)	244	544										
1959(2)	200	516	675									
1959(1)	270	375	455	455								
1958(2)	125	218	242	241	227							
1958(1)	...	188	197	204	198	181						
1957(2)	...	...	280	272	257	233	200					
1957(1)	...	...	...	422	380	330	260	190				
1956(2)	...	...	...	...	400	320	240	180	120			
1956(1)	...	...	...	...	...	340	260	180	125	80		
1955(2)	...	...	...	...	...	...	280	190	130	90	70	
1955(1)	...	...	...	...	...	...	...	190	130	90	50	30
1954(2)	...	...	...	...	...	...	...	...	165	90	50	25
1954(1)	...	...	...	...	...	...	...	...	...	72	43	20
1953(2)	...	...	...	...	...	...	...	...	...	...	44	20
1953(1)	...	...	...	...	...	...	...	...	...	...	...	20

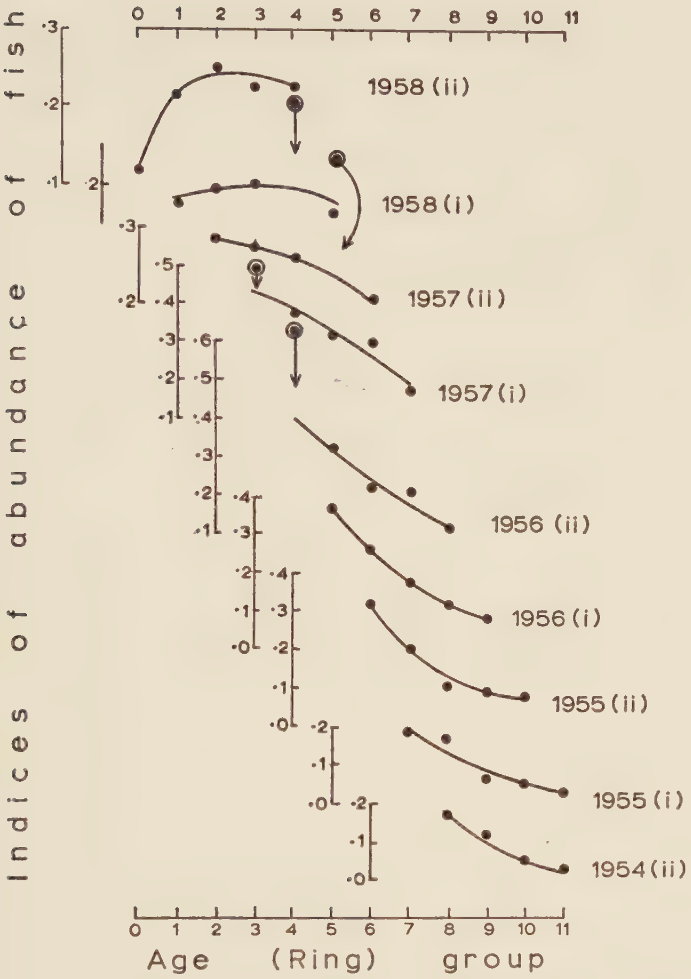

FIG. 4. The systematic change in the abundance of individual spawning groups. Data from Table VII-B.

Using these adjusted figures the catch curves for successive ring groups during each season of the study have been illustrated in Fig. 5. Fish entering the spawning stock at the end of 1956 and beginning of 1957 were relatively abundant and the progression of these strong spawning groups can be followed through the period, together with their diminishing contribution to the fishery. Since these estimates of abundance are based upon data adjusted for the selectivity of the gear, the figure does not represent the abundance of each age group in the catches and in fact this strong 1956/57 group did not make its main contribution to the catches until it was 4/5 seasons of age in 1959. It was followed by poor recruitment in 1958 but there are indications that a second strong group appeared in late 1959. It is estimated from the growth rate of juveniles that fish reach maturity at 2 years of age, so that this latter strong recruitment group may be directly related to that of 1956/1957.

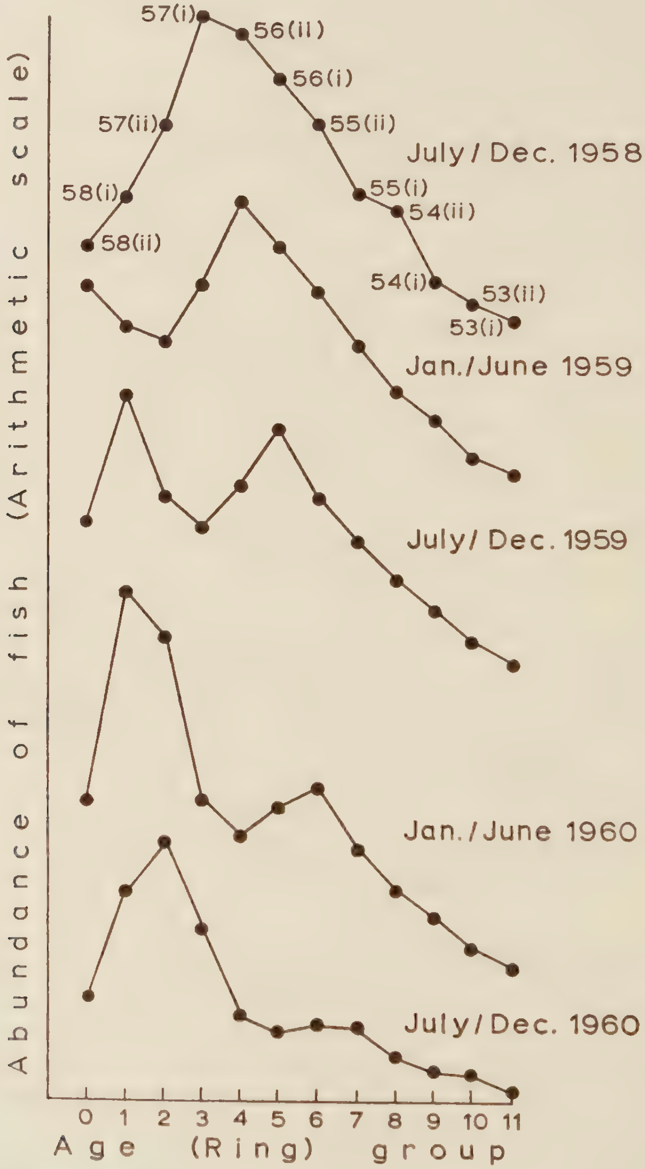

FIG. 5. Survival curves of the *T. esculenta* population during five successive seasons. Data from Table VII-B.

(5) CALCULATION OF TOTAL MORTALITY COEFFICIENTS

Total mortality coefficients were calculated from each pair of estimates of abundance of a ring group using expression 5 (page 197).

In carrying out this calculation allowance was made for recruitment to the age group at 26.0 cm length since these fish, regardless of their age, cannot be regarded as having been a part of the exploited stock prior to the season in which they first occur. At this length the growth of *T. esculenta* does not exceed 1 cm per 6-month period, so that only the one length group is affected. An example of the calculation is given in Table VIII where the July/December 1956 spawning group has an index of abundance of 400 at 4 rings, reduced to 320 at 5 rings. Of these latter, 28 or 8.7% are newly recruited at 26.0 cm (column 2, section B, Table VI), so that the survivors at 5 rings of those present in the exploited stock at 4 rings are 292. The mortality coefficient for this period is therefore $-\log_e (292/400) = 0.315$.

Table IX gives the total mortality coefficients for each of the 4 periods bracketed by the 5 estimates of abundance of each spawning group. Figure 6

TABLE VIII. Calculation of total mortality coefficients for the July–December 1956 spawning group.

Ring Group	Abundance (Table VII-B)	Recruits (Table VI)	No. of recruits	Initial abundance	Survivors	Mortality coefficient
		%				
4	400	4.4	18	...	292	0.315
5	320	8.7	28	292	215	0.397
6	240	10.3	25	215	177	0.305
7	180	1.4	3	177	120	0.406
8	120	0	0	120	...	...

TABLE IX. Total mortality coefficients based upon estimates of abundance given in Table VII-B.

	Seasons between rings											
Season	0/1	1/2	2/3	3/4	4/5	5/6	6/7	7/8	8/9	9/10	10/11+	Total
1960(1)	.033											
1959(2)	−.207	.403										
1959(1)	.568	.336	.700									
1958(2)	.083	.422	.377	.361								
1958(1)	...	.281	.190	.077	.207							
1957(2)	...	...	.175	.217	.115	.153						
1957(1)	...	...	...	.202	.201	.250	.342					
1956(2)	...	...	...	...	.315	.397	.305	.406				
1956(1)	...	...	...	...	...	.287	.401	.373	.446			
1955(2)	...	...	...	...	...	...	.415	.379	.368	.251		
1955(1)	...	...	...	...	...	...	...	.379	.368	.587	.511	2.677
1954(2)	...	...	...	...	...	...	...	...	.606	.587	.693	2.768
1954(1)	...	...	...	...	...	...	...	...	...	.516	.766	3.316
1953(2)	...	...	...	...	...	...	...	...	...	...	.788	3.508
Average				.214	.209	.272	.366	.384	.447	.485	.689	
Values from fitted line				.205	.210	.270	.350	.400	.445	.485	.520	2.885

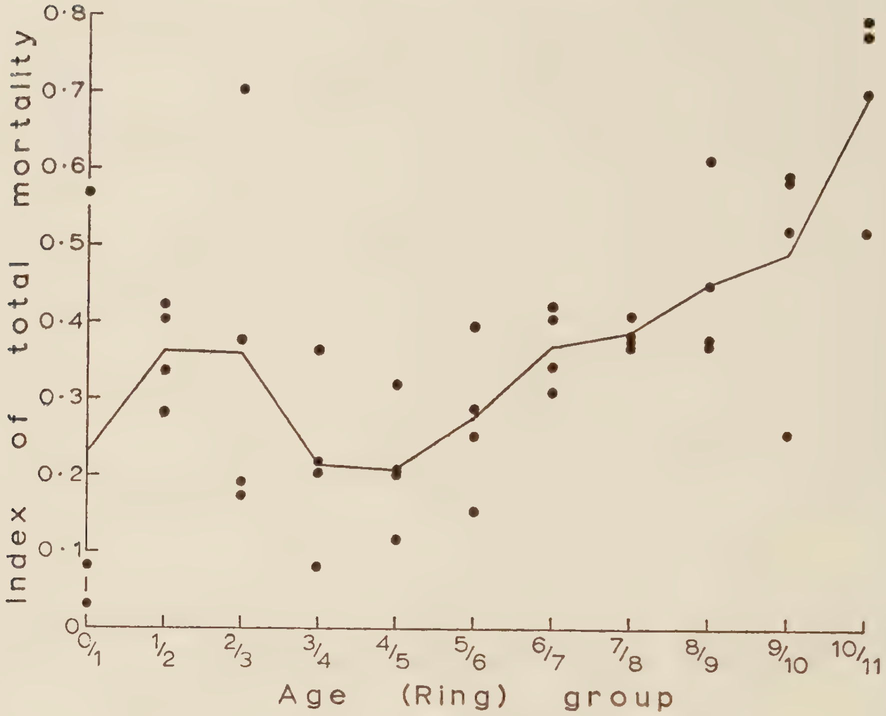

FIG. 6. Total mortality coefficients. Data from Table IX.

of these estimates shows that there was considerable variation in the mortality. If it is assumed that for any one age (ring) group the natural mortality[3] remains constant then a relationship should exist between these total mortality coefficients and the fishing effort. But, although natural mortality can be assumed constant within each 6-monthly period there may be a trend in its magnitude with increasing age. Even so, the relative change in mortality between ring groups will remain constant regardless of the fishing effort, so that it can be said that the sum of the total mortality coefficients for all ring groups within a season will be linearly related to the fishing effort. In fact, individual coefficients are subject to errors which are especially noticeable in those groups where recruitment is high, so that the summation technique has been applied only to ring groups ¾ upward. The summed total mortality coefficients are given in Table X with the mean monthly fishing effort for the 2 periods upon which the estimates are based.

There are clear indications of a linear relationship between these two variables, which are illustrated in Fig. 7 and a line has been fitted by eye to the 4 points. The line cuts the abscissa at approximately 1.750 so that, because fishing mortality is zero when the fishing effort is zero, this figure represents the changing natural mortality coefficients summed for the same ring groups.

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[3] Within the time period of 6 months per age group this is a reasonable assumption in this relatively stable typical environment, although it is also necessary to assume that the magnitude of M is independent of stock density.

TABLE X. Comparison of summed mortality coefficients (3/4 season upwards) with fishing effort.

Season	Summed total mortality	Fishing effort
1958(2) – 1959(1)	3.508	40,500
1959(1) – 1959(2)	3.316	32,000
1959(2) – 1960(1)	2.768	18,000
1960(1) – 1960(2)	2.677	20,500

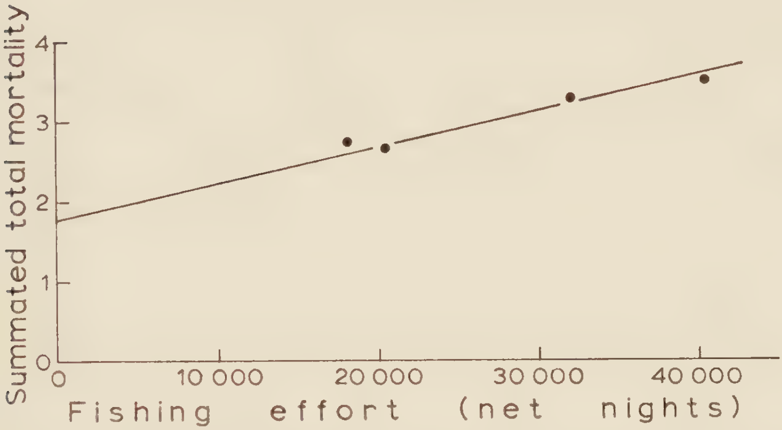

FIG. 7. The relationship between the fishing effort (gill net nights per month) and the total mortality. Data from Table X.

(6) SUBDIVISION OF THE SUMMED TOTAL MORTALITY COEFFICIENTS INTO THE COMPONENT FISHING AND NATURAL MORTALITY COEFFICIENTS FOR EACH AGE GROUP IN EACH SEASON

Using the argument put forward before, one can say that despite seasonal fluctuation of fishing effort, and therefore fishing mortality, the relative change of mortality between different ring groups during the same season will remain constant. This pattern of the total mortality is shown by the average mortality coefficient for each ring group given in Table IX. This is illustrated in Fig. 6 with a line fitted to the average coefficients. The average total mortality values for each ring group obtained by this adjustment are also given in Table IX.

These values can be subdivided from a knowledge of the variation in fishing mortality from age to age as deduced from the selectivity of the fishing gear.

(*i*) SELECTIVITY OF THE $4\frac{1}{2}$-INCH GILL NETS FOR AGE GROUPS (RING GROUPS)

The predetermined average growth curve of *T. esculenta* showed that the population is composed of fish with very similar growth rates but which mature at different lengths, causing their recruitment to the *exploited stock* to occur over a range of age, i.e. it requires longer for a fish maturing at 22 cm to grow into the exploited stock than a fish maturing at 25 cm.

The range of recruitment to the fishable stock is given by the distribution of size at maturation and a hypothetical population of 100 fish can be taken as having this size distribution when the first ring is laid down. Assuming no mortality of any form, the growth of these fish through subsequent seasons can be followed to give the number of fish in any length group for all ages. This is given in Table XI-A. In Table XI-B these theoretical abundance figures are multiplied by the gill net selection factor for each length group and the products summed for each ring group. The selection factor for size reflects the efficiency of the gill net relative to the mode and this treatment gives a selection factor for each age which is weighted according to the distribution of length within the appropriate ring group. The maximum fishing mortality for age using 4½-

TABLE XI-A. The number of fish at length for age, assuming a given initial population size with nil mortality.

Ring group	Midpoint of length groups—*cm*							
	26.5	27.5	28.5	29.5	30.5	31.5	32.5	33.5
0	7	2	1	1	1			
1	14	20	2	1	1			
2	32	14	13	9	1	1		
3	25	16	30	13	9	1	1	
4	7	25	16	30	20	2	1	
5	1	7	11	30	30	20	2	1
6	...	1	1	31	32	27	9	1
7	...	...	1	1	31	32	34	2
8	...	...	...	1	7	41	43	9
9	...	...	...	...	1	18	46	22
10	...	...	...	...	1	1	47	50

TABLE XI-B. Mortality for each age (ring) group: i.e., the gill net selectivity factor for each length multiplied by the number of fish of each ring group at each length.

	Midpoint of length groups, *cm*								Weighted mortality rating	Mid-point (%)
	26.5	27.5	28.5	29.5	30.5	31.5	32.5	33.5		
Factor:	19.1	51.6	89.5	98.0	82.6	46.9	25.5	10.3		
Age										
0	134	103	90	98	83	...	...	...	508	12.8
1	267	1032	179	98	83	...	...	...	1659	33.4
2	611	722	1164	882	83	47	...	...	3509	61.0
3	478	826	2685	1274	743	47	26	...	6079	90.0
4	134	1290	1432	2940	1652	94	26	...	7568	99.3
5	19	361	984	2940	2478	938	51	10	7781	98.3
6	...	52	90	3038	2643	1266	230	10	7329	83.5
7	...	...	90	98	2561	1501	867	20	5137	55.9
8	...	...	...	98	578	1923	1096	92	3787	37.3
9	...	...	...	...	83	844	1173	224	2324	25.7
10	...	...	...	...	83	47	1198	510	1838	18.0

inch gill nets will occur at an age of 5 rings (2.5 years in the exploited stock) and the efficiency of the net at other ages, referred to this, is illustrated in Fig. 8.

The mortality coefficients have been measured as occurring during the season and the selection for age factor relevant to a ring group has been taken at the mid-point during seasons, i.e. 0.5, 1.5, 2.5, 3.5, 4.5, etc., rings age on Fig. 8.

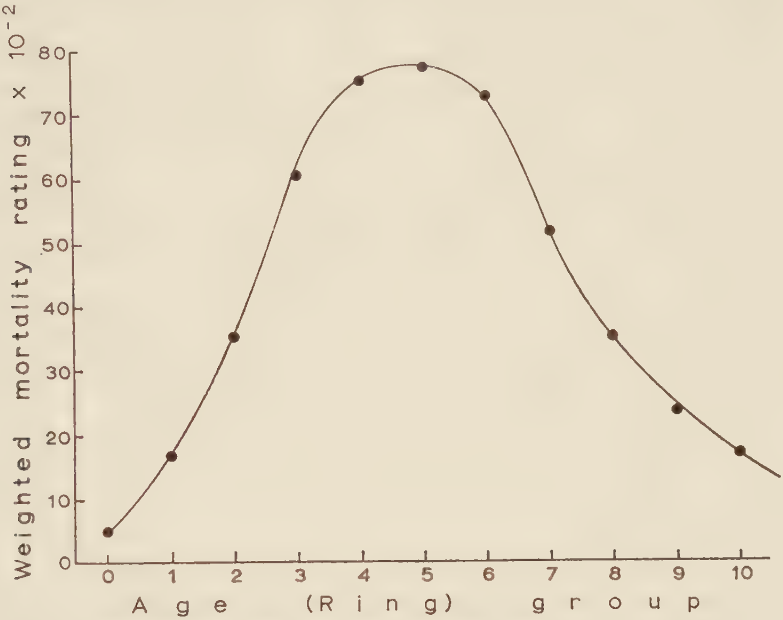

FIG. 8. The selection curve for age of 4½-inch nylon gill nets. Data from Table XI-B.

(*ii*) INTERACTION OF FISHING AND NATURAL MORTALITY

From the above analysis the pattern of both total mortality and fishing mortality is known for ages exceeding 3 rings. It is now possible to select trial values of fishing mortality at its maximum and to calculate the fishing mortality which would occur at each ring group. This value is then subtracted from the relevant total mortality estimate to give an estimate of natural mortality.

Taking the simplest assumption, one can say that natural mortality is zero for a period following maturation so that the fishing mortality at its maximum (5 rings) cannot be greater than a value giving a coefficient of approximately 0.200 at an age of 3 rings (0.205 being the calculated value of total mortality for fish of this age). Trial values of F, the fishing mortality coefficient at the length of maximum vulnerability, are given in Table XII-A; resultant values of natural mortality are shown in Table XII-B for each ring group, the pattern being determined as before.

Table XII-B shows that the value of F cannot *exceed* 0.225 without causing negative natural mortality when subtracted from the calculated total mortality coefficient. This is clearly impossible, but at F = 0.225 the value of M is

TABLE XII-A. Fishing mortality (F) at successive age (ring) groups for trial values of F at its maximum (5 rings)

Trial F	Ring group								
	3/4	4/5	5/6	6/7	7/8	8/9	9/10	10/11	Total
.200	.130	.199	.197	.167	.112	.075	.051	.036	1.017
.225	.202	.223	.221	.188	.126	.084	.058	.040	1.142
.250	.225	.248	.246	.209	.140	.093	.064	.045	1.270
.300	.270	.298	.295	.251	.168	.112	.077	.054	1.525
.350	.315	.348	.344	.292	.196	.131	.090	.063	1.779

TABLE XII-B. Values of natural mortality at trial values of (F) i.e. total mortality minus F at each age.

Trial F	Ring group								
	3/4	4/5	5/6	6/7	7/8	8/9	9/10	10/11	Total
.200	.015	.011	.073	.233	.288	.370	.434	.484	1.908
.225	.003	−.013	.049	.162	.274	.361	.427	.480	1.743
.250	−.020	−.038	.034	.141	.260	.352	.421	.475	. . .
.300	−.065	−.088	−.025	.099	.232	.333	.408	.466	. . .
.350	−.110	−.138	−.074	.058	.204	.314	.395	.457	. . .

initially low, and the summation of M for each ring group gives a total of 1.743. This corresponds very closely with the point at which the figure relating total mortality to fishing effort cuts the abscissa, thus supporting the accuracy of the estimate. Values of F at 0.200 *or lower* give a total M which is higher than 1.900. A trial value M = 1.750 has therefore been taken as a constant throughout the period of the study. From Fig. 7 the values of summed total mortality appropriate to the known fishing effort are 3.550, 3.150, 2.650 and 2.750 in the respective seasons, which by subtraction of the value for M give summed F values of 1.800, 1.400, 0.900 and 1.000 for those seasons. This total fishing mortality is then distributed between the relevant ring groups (3 and upwards) according to the data given in Table XI-B. The actual fishing mortality coefficients obtained are given in Table XIII.

TABLE XIII. Fishing mortality coefficients at successive ring groups between successive seasons, compared with fishing effort in gill net nights.

Season	Ring groups											Fishing effort
	0/1	1/2	2/3	3/4	4/5	5/6	6/7	7/8	8/9	9/10	10/11	
1958(2) to 1959(1)	.045	.118	.215	.318	.351	.349	.297	.198	.133	.090	.063	40,500
1959(1) to 1959(2)	.035	.092	.168	.247	.273	.272	.231	.154	.104	.070	.049	32,000
1959(2) to 1960(1)	.023	.059	.107	.158	.173	.173	.147	.098	.066	.044	.031	18,000
1960(1) to 1960(2)	.023	.065	.120	.176	.195	.194	.165	.110	.074	.050	.035	20,500

From the distribution of F between ring groups (Fig. 8) these coefficients are used to define the value of F at its maximum for each period. These are 0.353, 0.275, 0.176 and 0.196 respectively, and in fact values of F for ages 0/1, 1/2, and 2/3 rings have been entered by calculation from this maximum value. The maximum value of F is plotted against the relevant fishing effort in Fig. 9, where it can be seen that a straight line from the origin lies close to these 4 points. The deduced pattern of fishing mortality and natural mortality is illustrated in Fig. 10. The trend in natural mortality suggests that this may include some emigration of older fish which cannot be estimated.

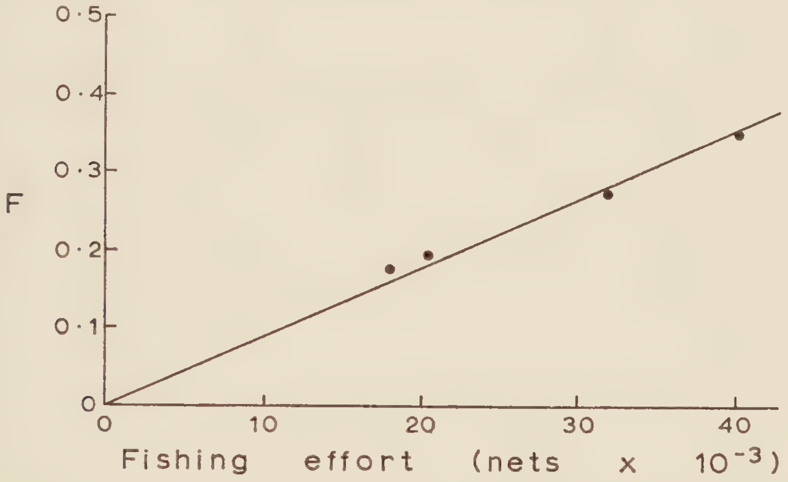

FIG. 9. The relationship between fishing mortality and the average monthly fishing effort.

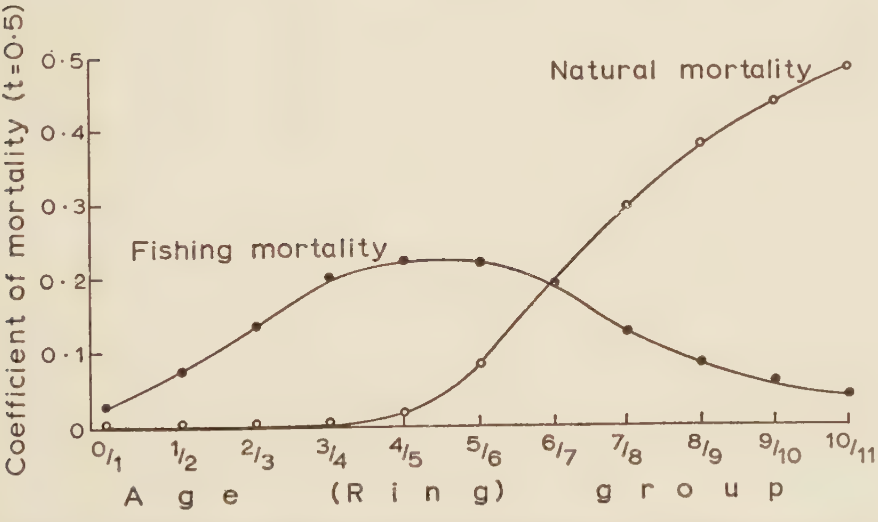

FIG. 10. The pattern of fishing mortality and natural loss in different age groups.

The fishing effort of 40,500 nets per month obtaining during the first season, would, if continued over a year, have given a yearly F value of 0.76 at the age of maximum vulnerability. This corresponds to the level of fishing mortality F = 0.75, estimated by Beverton during his visit in 1957 when the fishing effort was approximately the same. Further confirmation of the accuracy of these estimates of F, and their relationship to fishing effort, can be obtained by comparing the actual yield with the predicted yield obtained by using the relevant value of F against the estimate of abundance of the population.

(7) COMPARISON OF THE ACTUAL YIELD WITH THE PREDICTED YIELDS THAT WOULD BE OBTAINED USING THE CALCULATED ESTIMATES OF FISHING MORTALITY

The conversion of total catch records collected by the African fishguard to estimates of catch (yield) from each ring group is carried out in an exactly similar manner to the estimation of their abundance, with the exclusion of correction for the selectivity of the fishing gear. The total catch for each month was subdivided according to the relative representation of each length group and the yield for each length group was then treated to give a monthly average for each 6-month period. These yields were then re-divided according to the age (ring) composition of each length group and the yield of each ring group then summed over the length range.

The average yields for the relevant periods for which fishing mortality coefficients have been calculated are given in Table XIV. The calculation of the predicted yields is given in Table XV, which represents a complete model of changes in this population of *T. esculenta* since the second half of 1958.

TABLE XIV. Average monthly yield for each period (number of fish).

Ring Group	1958(2) –1959(1)	1959(1) –1959(2)	1959(2) –1960(1)	1960(1) –1960(2)
0	3,069	2,975	1,650	2,236
1	3,654	3,823	3,760	4,540
2	5,447	3,704	2,830	4,808
3	9,398	5,368	2,231	3,401
4	11,844	7,256	3,228	3,175
5	8,059	6,163	3,139	2,621
6	6,116	4,802	2,293	2,396
7	3,292	2,879	1,493	1,726
8	2,391	1,932	798	992
9	1,011	972	517	623
10	583	610	276	494
11+	218	256	159	182
Total	55,082	40,740	22,374	27,194

In Table XV the first set of figures in column 2 represents the average adjusted numerical abundance of each ring group in the population during the period in which the study began (the second half of 1958), from Table VII-B,

TABLE XV. Theoretical model of the Waigalla population of *T. esculenta*. For explanation see the text.

1 Ring group	2 Abundance	3 F	4 Yield	5 M	6 Natural loss	7 Survivors	8 Survivors in next season	9 Required recruits	10 Actual recruits	11 Abundance next season
	no.		*no.*		*no.*	*no.*	*no.*	%	%	*no.*
A. 1958(2)										
0	125	.045	6	.005	1	118	...	100.0	100.0	270
1	188	.118	21	.005	1	166	118	45.9	49.1	218
2	280	.215	54	.005	1	225	166	15.7	27.9	197
3	422	.318	115	.005	2	305	225	19.1	13.6	272
4	400	.351	118	.005	2	280	305	19.7	9.1	380
5	340	.349	100	.049	16	224	280	12.0	8.9	320
6	280	.297	72	.162	42	166	224	13.0	1.9	260
7	190	.198	34	.274	46	110	166	13.0	2.4	190
8	165	.133	21	.361	50	94	110	...	...	130
9	72	.090	6	.427	25	41	94	...	...	90
10	44	.063	3	.480	17	24	41	...	...	43
11	20	...	...	...	...	...	24	...	...	20
Total	...	...	550	...	...	...	...	...	...	...
B. 1959(1)										
0	270	.035	9	.005	1	260	...	100.0	100.0	200
1	218	.092	19	.005	1	198	260	30.7	59.3	375
2	197	.168	30	.005	1	166	198	18.2	41.1	242
3	272	.247	60	.005	1	211	166	18.6	20.0	204
4	380	.273	91	.005	2	287	211	17.9	14.8	257
5	320	.272	76	.049	15	229	287	13.0	5.8	330
6	260	.231	54	.162	39	167	229	4.6	10.3	240
7	190	.154	27	.274	46	117	167	7.2	2.8	180
8	130	.104	13	.361	39	78	117	...	...	130
9	90	.070	6	.427	31	53	78	...	...	90
10	43	.049	2	.480	16	25	53	...	...	50
11	20	...	...	...	...	...	25	...	...	20
Total	...	...	387							
C. 1959(2)										
0	200	.023	5	.005	1	194	...	100.0	100.0	244
1	375	.059	21	.005	2	352	194	63.4	52.3	516
2	242	.107	38	.005	1	203	352	22.6	41.1	455
3	204	.158	30	.005	1	173	203	15.8	31.3	241
4	257	.173	41	.005	1	215	173	12.6	4.4	198
5	330	.173	52	.049	16	262	215	7.7	1.5	233
6	240	.147	33	.162	36	171	262	...	1.0	260
7	180	.098	17	.274	43	120	171	5.0	1.4	180
8	130	.066	8	.361	39	83	120	...	...	125
9	90	.044	4	.427	31	55	83	...	...	90
10	50	.031	2	.480	19	29	55	...	...	50
11	20	...	...	...	...	...	29	...	...	25
Total	...	...	251							
D. 1960(1)										
0	244	.025	6	.005	1	237	...	100.0	100.0	264
1	516	.065	32	.005	3	481	237	56.4	56.2	544
2	455	.120	51	.005	2	402	481	28.7	48.9	675
3	241	.176	39	.005	1	201	402	9.7	49.2	445
4	198	.195	35	.005	1	162	201	11.4	25.8	227
5	233	.194	41	.049	11	181	162	10.5	...	181
6	260	.165	40	.162	38	182	181	9.5	...	200
7	180	.110	19	.274	43	118	182	4.2	4.0	190
8	125	.074	9	.361	38	78	118	...	...	120
9	90	.050	4	.427	31	45	78	...	...	80
10	50	.035	2	.480	19	29	45	...	...	70
11	25	...	...	...	...	...	29	...	...	30
Total	...	...	278							

in terms of 1,000 times the catch per net. This was exploited by a fishing effort causing a fishing mortality F = 0.353 per half year at the most vulnerable age; F values for successive ring groups shown in column 3 are taken from Table XIII. The product of columns 2 and 3 gives the yield for each ring group, shown in column 4. Natural mortality caused a further loss from the population which is computed similarly in columns 5 and 6. The survival from each ring group is then given by column 7, being column 2 less columns 4 and 6. These fish represent the potential population of the following season when they will be one ring older. This adjustment of age is given by column 8, which can be directly compared with the independent estimate of abundance for the following season, in column 11. However, new recruits are added to the survivors from the first season and column 9 gives the percentage of the abundance in the coming season that is required to make up the numbers. In column 10 this percentage is compared with the observed percentage calculated from Table VI in the same way as in column 3 of Table VIII. This procedure is repeated for all seasons using the F values appropriate to each, from Table XIII. The computation finishes finally with the abundance of stock in the July/December 1960 period.

It can be seen that in each season the required proportion of recruits has the same order of magnitude as the observed recruitment. The correspondence is not in all cases very exact but it should be remembered that small errors in the estimates of F could cause the number of survivors from one season to exceed their abundance in the following season, as this latter is an independent estimate. This has not occurred.

Table XVI gives a comparison between the predicted and actual yields of the fishery, together with a repetition of relevant ancillary data.

TABLE XVI. A comparison of theoretical and actual yields for the fishery.

Season	Fishing effort (monthly average)	F (max.)	Actual yield	Yield relative to 1st season	Theoretical yield	Yield relative to 1st season	Total theoretical abundance
	net-nights		*no.*		*no.*		*no.*
1958(2)–1959(1)	40,500	0.353	55,000	1.00	550	1.00	2526
1959(1)–1959(2)	32,000	0.275	40,500	0.74	387	0.70	2370
1959(2)–1960(1)	18,000	0.176	22,000	0.40	252	0.46	2382
1960(1)–1960(2)	20,500	0.196	27,000	0.49	278	0.51	2617

The changes in actual average monthly yield from season to season bear a very close similarity to the predicted yields, and in Fig. 11 the predicted and actual yields are illustrated according to the yield from each ring group. For most ring groups the correspondence is extremely accurate, but there is a degree of inaccuracy for the 0 and 1 ring groups. For these groups the observed yield can only be obtained in theory by assuming a substantial increase in the value of F which, owing to the selectivity of the gear, would indicate comparable increases in F at other ring groups. This is clearly not so and the most probable explana-

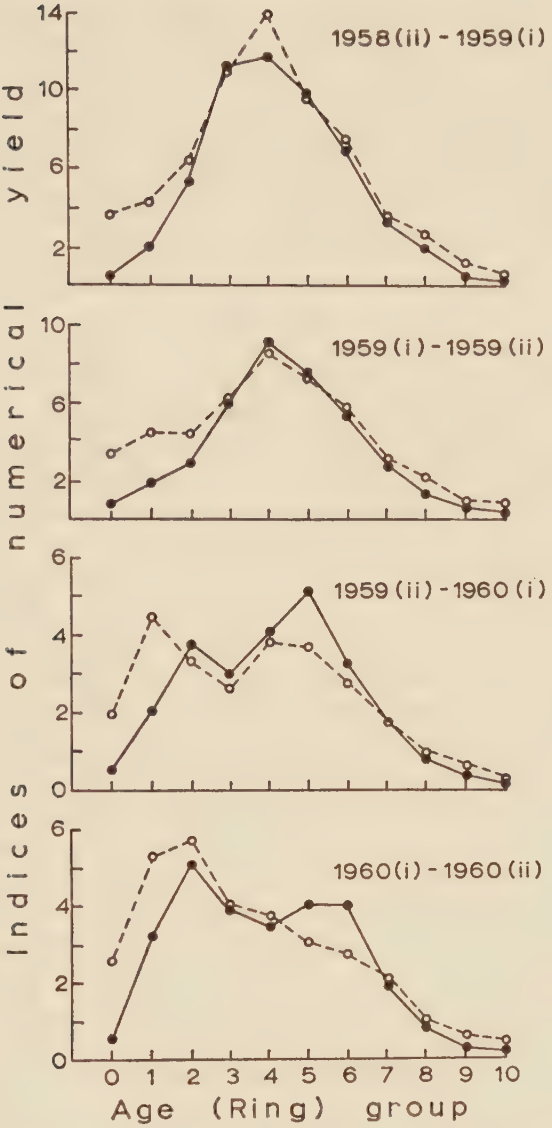

FIG. 11. The comparison between the actual and predicted yields. Open circles: actual yield; black circles: predicted yield. Data from Table XV.

tion of the underestimate of predicted yield from the smaller fish is a change in the behaviour which influences the selectivity of the gear. There was some indication of this when the selection pattern of the gear was determined; the regression of the log ratios of catches at successive length groups against length had a degree of sigmoid asymmetry at the extremes of the selection range which could not be accurately determined (see Garrod, 1961).

The early ring groups are recruited from shoals swimming in open water, and presumably, after recruitment they still have a greater tendency to shoaling than older breeding fish. The likelihood of capture of fish moving in a shoal is very much higher than if fish are moving in a random fashion, so that greater catches may be expected from the younger age groups showing shoaling behaviour (Lowe-McConnell, 1956; Baerends and Baerends van Roon, 1950). Indeed the tendency of these fish to be caught in clusters in a gill net has been noted on many occasions during experimental fishing.

DISCUSSION

The complex steps which are necessary in estimating the true abundance of fish etc., all introduce small errors which must accumulate, so that it would be pretentious to suggest that the fishing mortality coefficients calculated above are accurate to three significant figures. Nevertheless, the estimates do provide the basis of a model which predicts logically all the observed changes in the fishery. Furthermore there is a linear relationship between the values of F and the magnitude of fishing effort. These facts confirm the general accuracy of the estimates.

The purpose of this paper is to demonstrate the method of computing mortality estimates from evidence taken by analysis of a gill net fishery and to show the data required so that similar work may be carried out elsewhere in Africa.

From the results outlined above it is possible, knowing the relationship between effort and mortality, to calculate a complete theoretical model of the fishery showing the level of effort at which catch numbers or weight can be maximised, and the effect of changing fishing gear, etc., with all its economic implications. This will be given in a later publication, but several points of general interest have arisen.

(1) This study provides a demonstration of the use of a knowledge of the selectivity of the gill net to determine the natural mortality from a total mortality coefficient. Its use could be a standard technique for the determination of M to compare with the results from tagging experiments. The form of natural mortality for mature *T. esculenta* is itself interesting in being initially very low and showing a rapid increase after fish have been in the fishable stock for $2\frac{1}{2}$ years. It has been noticed that this may include a degree of emigration of these fish.

(2) The extreme selectivity of a gill net restricts the efficiency of cropping to a very narrow length and age range. This is particularly evident for lower ring groups where recruitment is good. For example, in the July/December 1959 season the abundance of 1-ringers and 5-ringers in the population was comparable yet the yield from the latter was $2\frac{1}{2}$ times greater because of the selectivity of the gear. This in itself may be an advantage in allowing fish to survive to a marketable size, because 1-ringers are approximately $\frac{3}{4}$ lb (340 g) compared to 1–$1\frac{1}{4}$ lb (450–570 g) at 5 rings.

The narrow age band of efficient exploitation also means that during any one season the fishing is heavily dependent upon the recruitment approximately 2½ years previously.

(3) The level of fishing mortality at its maximum is not excessive and applies only to a narrow age band. Other ages are subject to considerably less mortality. It was shown earlier that, should fishing effort average 40,000 net nights per month for a year, the value of F would be approximately 0.70. This value is comparable to Beverton's earlier estimate and also to the F value for the North Sea plaice fishery. However, this latter fishery is carried out by trawling and Danish seining which have only a lower selection limit, i.e. are not doubly selective, so that all ages following recruitment to the exploited stock are subject to the same value of F. This is not so with a gill net fishery, where most age groups are subject to F values considerably lower than the maximum.

(4) The pattern of selectivity causes only small changes in the mortality of the very old fish, despite extensive variation in the total fishing effort. Throughout the study small numbers of fish have survived more than 5 years in the exploited phase and have almost grown beyond the effective selection range of the gear (to a size of about 33.0–34 cm). This explained the very small numbers of fish caught at lengths exceeding 34.0 cm because, having survived to this age, they can be regarded as having passed out of the stock exploited with 4½-inch nets.

(5) The comparison between exploitation of plaice and *T. esculenta*, which was given above as indicating a relatively low rate of exploitation of the latter, assumes that *T. esculenta* can maintain its rate of recruitment. The species is a mouth brooder producing relatively few eggs which have a high percentage survival compared to species producing many eggs. It may be that *T. esculenta* is unable to maintain its recruitment rate under intense exploitation.

(6) One of the primary results of this study has been to show that, despite the lack of a well defined seasonal environmental regime in Lake Victoria, the progress of biological processes is cyclical as in temperate lakes and that normal techniques of analysis are applicable to the data.

SUMMARY

(1) The coefficients of fishing mortality for a unit stock of *T. esculenta* in the Jinja/Waigalla area of Lake Victoria have been estimated for 4 seasons.

(2) The relationship between fishing effort and the resulting fishing mortality have been defined.

(3) The method of determining these mortality coefficients is described in detail. It is carried out in a series of steps.

(a) Estimation of the length frequency distribution of commercial catches.

(b) Correction of catch data for each length group by a factor compensating for the selectivity of gill nets, giving the actual abundance of each length group.

(c) The abundance of each length group is sub-divided according to the age composition of each length group.

(d) The abundance of each age group in each length group is summed to give the true abundance of each age group.

(e) The changing abundance of one spawning group is traced with its progress through several seasons.

(f) Total mortality coefficients are calculated during each season for each age group.

(g) The total mortality coefficients for each age group are then summed through one fishing season to give a summed total mortality coefficient for that season.

(h) This summed coefficient is related to the fishing effort in each season and the total natural mortality coefficient deduced graphically from the relationship.

(i) The natural mortality has been assumed to remain constant and has been deducted from the summed total mortality rating to give the summed fishing mortality, which is distributed through the age groups according to the selectivity of the gear.

(4) The accuracy of these determinations is confirmed by using them in a theoretical model of the fishery which gives patterns of recruitment and yield similar to those observed in practice.

(5) The general implications of these findings are discussed for the *T. esculenta* fishery of Lake Victoria.

(6) The value of using gill nets as a technique in determining natural mortality is emphasised.

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Nutrient Composition and Evaluation of British Columbia Whole Herring Meal[1,2]

By B. E. March and J. Biely

Poultry Science Department,
University of British Columbia

and

H. L. A. Tarr

Fisheries Research Board of Canada,
Technological Station, Vancouver 8, B.C.

ABSTRACT

Six composite samples of British Columbia whole herring meals representative of the 1960–1961 commercial production were analyzed for protein, fat (ether extract), ash, water, minerals, vitamins of the "B complex", available lysine, 13 amino acids and protein digestibility. The biological availability of the protein was also checked by determining the supplementary protein value for chicks. The results, which are tabulated and discussed, indicate that the herring meals were of comparatively consistent composition and of high nutritional value.

INTRODUCTION

Fish meals as a class vary considerably on the basis of both their proximate analysis and with regard to their nutritive properties. The variations are the consequence of differences in the type of fish used and in the methods of manufacture. Unfortunately, and all too frequently, scientific papers dealing with the nutritive value of fish meals have neglected to mention the variety of fish meal used in the tests reported, the origin of the meal or specific nutritional data regarding it. Then too, much of the analytical data available in the literature is based on the results of studies made before standard assay techniques had been developed for the nutrients in question. With respect to biological evaluation of fish meal much of the information in the literature is based on tests conducted before our knowledge of nutrition had reached its present status. It is accordingly difficult to evaluate the results obtained in many experiments although in some cases re-evaluation and explanation of the data is possible in the light of present knowledge. Despite the vast amount of research that has been done on fish meals there are still many gaps in our knowledge of their amino acid, vitamin and mineral composition. As already stated, fish meals as a class are of variable composition. Nevertheless, fish meal production in British Columbia

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[1] Received for publication August 29, 1962.

[2] This study was initiated by the Fisheries Association of British Columbia and was financed by the Industrial Development Service of the Department of Fisheries of Canada, the above Association, and the Fisheries Research Board of Canada.

J. Fish. Res. Bd. Canada, **20**(1), 1963.
Printed in Canada.

is practically limited to the manufacture of meal from whole herring. Also, the manufacture of the meals is carried out in a relatively small number of plants. The raw material is therefore of a uniform nature except for seasonal fluctuations in body composition related to the sexual maturity of the fish. For these reasons, a study with the object of providing a complete analysis of the nutrient composition of British Columbia herring meal was undertaken.

A recent report (Tarr, 1960) outlined some of the known nutritional properties of B.C. herring meal as well as of certain Atlantic herring meals. In that report all information given concerning B.C. herring meals was for so-called "standard" meals that are prepared by drying press-cake after removal of the press-water. The method of manufacture generally used has recently changed, and, as a result, nearly all of the herring meals produced to-day in British Columbia are "whole" or "full" meals, and are prepared by drying press-cake to which the solubles from the press-water has been added. The analytical data in the literature are, except in specified cases, concerned with press-cake meals and are, therefore, not applicable to whole meals. The fact that there is virtually no information regarding the amino acid, vitamin and mineral content of B.C. whole herring meals provided another important reason for an analytical study of these meals.

Tabulation of analytical data on fish meals accumulated from the literature has always necessitated comparison of values obtained from different groups of samples. Thus, one investigator may have studied riboflavin levels in a set of meals and the resultant values may be tabulated with the vitamin B_{12} levels in an entirely different set of meals. One object of the present study was to obtain amino acid, vitamin and mineral analyses from a single set of meals.

RESULTS

Since the purpose of the study was to provide data as comprehensive as possible on the nutrients present in B.C. herring meals, a special sampling procedure was devised. In British Columbia, the bulk of the herring meal is produced between October and the end of March. In 1960 the season opened in November, and a continuous sampling programme was initiated in the major herring meal plants in order to obtain representative samples of the daily production. These samples were kept in closed containers and were identified by the name of the processing plant, the date of manufacture, and the number of sacks of meal represented by the sample. These samples were subsequently pooled so as to obtain six large samples covering successive manufacturing periods during the production season. The following six periods were chosen as giving a representative cross-section of the entire season: November 23 to November 30, 1960; December 1 to December 7, 1960; December 8 to December 19, 1960; January 17 to January 26, 1961; January 27 to February 7, 1961; and February 17 to March 5, 1961.

The six pooled samples were analyzed by contract with the Wisconsin Alumni Research Foundation, Madison, Wisconsin. Standard methods (A.O.A.C., 1960) were used for the determination of protein (p. 12), protein digestibility

(p. 286), sodium (p. 76), potassium (p. 76), sulphur (p. 84), copper (p. 310), riboflavin (p. 669), thiamine (p. 655), niacin (p. 667) and folic acid (p. 830). The following additional methods were employed: calcium (Angols and Murray, 1949); phosphorus (Fiske and Subbarow, 1925); magnesium (Harvey, Komarny and Wyatt, 1953); iodine (Binnerts, 1954); manganese, cobalt, zinc and molybdenum (Sandell, 1959), amino acids by microbiological methods (Henderson and Snell, 1948), available lysine (Carpenter, 1960); pantothenic acid (Neilands and Strong, 1948); biotin (Wright and Skeggs, 1944); vitamin B_{12} (Anon., 1960); vitamin K (Almquist, 1941) and supplementary protein value (March and Biely, unpublished). Chick biological assays of the meals for their supplementary protein value (S.P.V.) and chemical assays for available lysine and other chemical analyses were carried out by the Department of Poultry Science of the University of British Columbia. The proximate analyses of the composite meals are shown in Table I.

TABLE I. Proximate analyses of six composite samples of B.C. whole herring meal.

Sample	Protein	Ether-extract	Ash	Moisture
	%	%	%	%
Nov. 23 to Nov. 30	72.12	8.4	10.55	7.66
Dec. 1 to Dec. 7	71.56	7.7	11.42	7.61
Dec. 8 to Dec. 19	71.68	7.8	11.25	7.51
Jan. 17 to Jan. 26	71.06	7.6	11.30	7.34
Jan. 27 to Feb. 7	70.56	8.3	11.20	7.93
Feb. 17 to Mar. 5	72.43	7.5	10.50	8.39
Average:	71.57	7.9	11.04	7.74

The herring meals averaged over 71% protein, thus being one of the richest sources of supplementary protein available for poultry rations. The levels of 13 amino acids in each composite sample are shown in Table II, together with the average values. Whether or not the amino acid composition of any protein concentrate is rated highly, depends, not upon a comparison of the levels of the essential amino acids with the levels required by the chicken, but upon how effectively the amino acid pattern of the concentrate complements the amino acid pattern of the cereal components of the ration to give a balanced pattern in the ration as a whole. To illustrate this point, Fig. 1 shows graphically the amino acid balance in rations based on various combinations of B.C. whole herring meal, soyabean oil meal, wheat, and yellow corn. The areas above the requirement line for each amino acid represent amounts of the amino acid supplied by the cereal–protein concentrate mixture beyond that required by the growing chick in a 20% protein diet; the areas below the requirement lines correspondingly represent deficiencies. The protein levels in the wheat, corn, soyabean oil meal and B.C. whole herring meal were taken to be 12, 8.8, 50, and 72% respectively. The calculations were made for a 20% protein ration in which the cereal and protein concentrate constituted 95% of the ration.

TABLE II. Amino acid content of six composite samples of B.C. whole herring meal (grams per 16 grams of nitrogen).

Production dates of composite samples	Nov. 23 to Nov. 30		Dec. 1 to Dec. 7		Dec. 8 to Dec. 19		Jan. 17 to Jan. 26		Jan. 27 to Feb. 7		Feb. 17 to Mar. 5		Average g/16 gN
		% in meal		% in meal		% in meal		% in meal		% in meal		% in meal	
Arginine	7.15	(5.16)	7.63	(5.46)	8.47	(6.07)	7.77	(5.52)	7.84	(5.53)	8.16	(5.91)	7.84
Lysine	7.97	(5.73)	8.06	(5.77)	8.10	(5.81)	8.78	(6.24)	8.47	(5.98)	7.68	(5.56)	8.18
Methionine	2.72	(1.96)	2.75	(1.97)	2.71	(1.94)	2.73	(1.94)	2.69	(1.90)	2.64	(1.91)	2.71
Cystine	0.987	(0.712)	1.02	(0.728)	1.03	(0.742)	1.03	(0.732)	0.981	(0.692)	1.03	(0.746)	1.01
Histidine	2.69	(1.94)	2.74	(1.96)	2.65	(1.90)	2.70	(1.92)	2.66	(1.88)	2.54	(1.84)	2.66
Tryptophan	0.976	(0.704)	0.878	(0.628)	0.932	(0.668)	0.913	(0.649)	0.845	(0.596)	0.889	(0.644)	0.905
Tyrosine	2.93	(2.11)	3.23	(2.31)	3.10	(2.22)	2.28	(1.62)	2.24	(1.58)	3.05	(2.21)	2.80
Isoleucine	4.37	(3.15)	4.16	(2.98)	3.99	(2.86)	4.16	(2.96)	4.05	(2.86)	4.32	(3.13)	4.17
Leucine	7.76	(5.60)	7.15	(5.12)	7.00	(5.02)	7.15	(5.08)	6.97	(4.92)	7.18	(5.20)	7.20
Phenylalanine	3.84	(2.77)	3.63	(2.60)	3.49	(2.50)	3.38	(2.40)	3.29	(2.32)	3.75	(2.72)	3.56
Threonine	3.97	(2.86)	4.09	(2.93)	3.75	(2.69)	4.02	(2.86)	4.10	(2.89)	4.06	(2.94)	4.00
Valine	7.67	(5.53)	8.05	(5.76)	7.69	(5.51)	8.25	(5.86)	8.28	(5.84)	7.54	(5.46)	7.91
Glycine	7.18	(5.18)	6.71	(4.80)	6.96	(4.99)	7.64	(5.43)	7.81	(5.51)	7.14	(5.17)	7.24
Percentage crude protein (N × 6.25)	72.12		71.56		71.68		71.06		70.56		72.43		

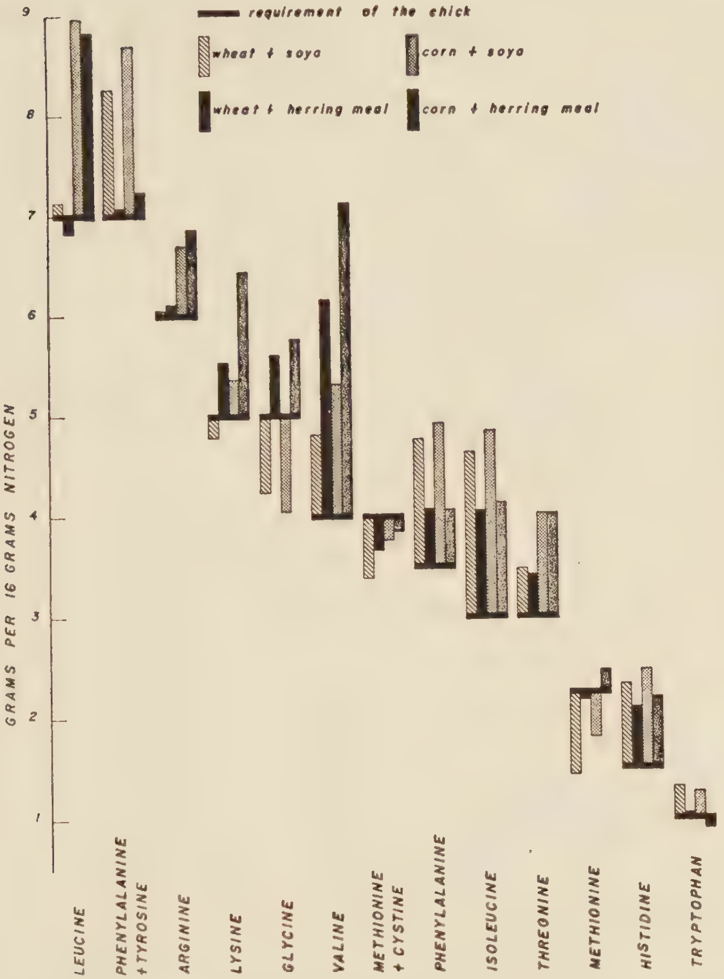

FIG. 1. Requirements of essential amino acids by chicks as met by rations based on various combinations of B.C. whole herring meal, soyabean meal, wheat and yellow corn.

It will be seen that the amino acids which are apt to be critical in a chick starting ration using wheat, corn, herring meal and soyabean oil meal are leucine, phenylalanine + tyrosine, arginine, lysine, glycine, methionine and tryptophan. Of these a deficiency of leucine may be encountered in rations containing wheat as the only cereal, but it is unlikely if some corn is included in the ration. It is difficult to formulate a ration of natural ingredients which will supply sufficient methionine or methionine + cystine. This general deficiency of methionine in feedstuffs has led to the common practice of adding synthetic methionine to broiler rations. Suboptimal levels of arginine and lysine may limit growth when the proportion of cereal protein to supplementary protein is high. In this connection herring meal is a better supplement than soyabean oil meal. Herring meal has the further advantage of being higher in glycine than soyabean oil meal. Fig. 1 shows that the all-vegetable rations are deficient in glycine for the chick, which, in contrast to the rat, requires this amino acid in the diet for normal growth rate. Phenylalanine + tyrosine and tryptophan levels are somewhat higher in rations containing herring meal as sole source of supplementary protein. Most effective supplementation of cereal protein is effected when a combination of soyabean oil meal and herring meal is used. Thus when herring meal and soyabean meal are used to contribute equal amounts of supplementary protein the only amino acids which are not present in the required amounts are methionine and cystine.

In Table III are given the estimates of protein digestibility based on the results of an *in vitro* enzyme digestion technique. The nitrogenous material not solubilized by the enzyme action, which would include keratins, is assumed to be of little or no value nutritionally.

TABLE III. *In vitro* protein digestibility and available lysine content of six composite samples of B.C. whole herring meal.

Sample	Digestibility	Available lysine
	%	g/16 gN
Nov. 23 to Nov. 30	93.0	7.4
Dec. 1 to Dec. 7	92.3	7.1
Dec. 8 to Dec. 19	92.2	6.7
Jan. 17 to Jan. 26	92.1	7.0
Jan. 27 to Feb. 7	92.7	7.2
Feb. 17 to Mar. 5	92.0	6.5
Average:	92.4	7.0

Also listed in Table III are the percentages of chemically determined available lysine. The average value obtained of 7.0% of the total protein is in accord with values given in the literature for good herring meals. Differences in the amount of available lysine present in the several composite samples are possibly due to differences in the degree of exposure to air during mixing, sampling and storage of the pooled samples.

The supplementary protein values (S.P.V.) of the meals are given in Table IV. This value is an expression of the supplementary protein value relative to a reference protein (96.7% isolated soyabean protein + 3.3% DL-methionine), assigned a value of 100. The composition of the basal diet used in the test is as follows: ground wheat 85.0 lb, limestone 1.25 lb, bonemeal 2.0 lb, and iodized salt 0.5 lb per 100 lb; manganese sulphate 6.0 g, menadione 0.22 mg, riboflavin 1.3 mg, calcium pantothenate 4.2 mg, pyridoxine-HCl 1.3 mg, biotin 0.04 mg, folic acid 0.25 mg, choline chloride 600 mg, α-tocopheryl acetate 6 mg, vitamin B_{12} 600 μg, vitamin A 2000 U.S.P. units and vitamin D_3 120 I.C.U. per lb.

The protein supplements are added to the basal diet to supply 8% of protein. The amount of bonemeal included in the diet is adjusted depending upon the mineral content of the fishmeal. The total weight of the diet is adjusted to 100 lb with dextrose. Growth rates of the chicks fed the rations are compared when the chicks are 4 weeks of age. The average S.P.V. of British Columbia whole herring meal was 122 and the differences among the composite meals were not statistically significant.

TABLE IV. Supplementary protein value (S.P.V.) of six composite samples of B.C. whole herring meal. There are no statistically significant differences in the values obtained for the different composite meals.

Sample	S.P.V.
Nov. 23 to Nov. 30	120
Dec. 1 to Dec. 7	127
Dec. 8 to Dec. 19	123
Jan. 17 to Jan. 26	116
Jan. 27 to Feb. 7	120
Feb. 17 to Mar. 5	124
Average:	122

VITAMINS

The results of analysis of the herring meals for 9 vitamins are presented in Table V. Since the meals were whole meals it was to be expected that they would contain relatively large amounts of water-soluble vitamins. In press-cake herring meal there is, of course, considerable loss of vitamins in the press-water. The levels of 6 of the B-complex vitamins in the meals tested, relative

TABLE V. Vitamin analyses of six composite samples of B.C. whole herring meal.

Vitamins	Production dates of composite samples						Average
	Nov. 23 to Nov. 30	Dec. 1 to Dec. 7	Dec. 8 to Dec. 19	Jan. 17 to Jan. 26	Jan. 27 to Feb. 7	Feb. 17 to Mar. 5	
(mg/100 g)							
Riboflavin	1.07	1.02	1.00	1.25	1.26	1.35	1.16
Pantothenic acid	1.89	1.89	1.87	2.12	2.10	2.74	2.10
Thiamine*	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Niacin	9.48	9.84	8.49	7.86	7.65	6.99	8.38
Folic acid*	ca. 0.1	ca. 0.1	ca. 0.1	ca. 0.1	ca. 0.1	ca. 0.1	ca. 0.1
Biotin	0.059	0.053	0.055	0.058	0.061	0.072	0.060
Choline	635.0	503.0	501.0	600.0	555.0	686.0	580.0
Vitamin B-12	0.042	0.045	0.047	0.044	0.048	0.053	0.046
Vitamin K	0.45	<0.1	0.45	<0.1	<0.1	<0.1	<0.1 to 0.45

* Accurate results for thiamine and folic acid were not possible due to sample interference at the required assay levels. Values indicated are estimated.

to the requirements of the chick from 0–8 weeks of age, are given in Table VI. Thiamine has been omitted from the table since herring meal cannot be considered a source. Folic acid, likewise, has not been included. Although raw fish contains appreciable folic acid, fish meals are unreliable sources. The vitamin is heat-labile and consequently is destroyed under normal fish meal processing conditions. With carefully controlled low temperature drying it is, however, possible to produce herring meal containing nutritionally significant levels of folic acid.

Special mention should be made of the vitamin K content of herring meal. Since it was first reported that fermented fish meal showed vitamin K activity, fish meals have frequently and erroneously been considered to be an important source of vitamin K in poultry rations. That this is not always the case has been demonstrated by experiments in which a state of vitamin K deficiency has been induced in chicks fed a diet containing herring meal as the sole source of supplementary protein (Davies *et al.*, 1958). These earlier observations are borne out by the analytical variation noted in the present meals.

TABLE VI. Levels of B-complex vitamins contributed to a ration by the inclusion of 10% B.C. whole herring meal.

	Chick requirement	B.C. whole herring meal	Chick requirement supplied by 10% herring meal
	mg/lb.*	mg/lb.	%
Riboflavin	1.3	5.27	41
Pantothenic acid	4.2	9.53	23
Niacin	12.0	37.86	32
Biotin	0.04	0.272	68
Choline	600.0	2633.0	44
Vitamin B-12	0.004	0.209	520

* National Research Council requirements for poultry.

MINERALS

Today there is a tendency in formulating poultry feeds to use fewer and fewer major ingredients in any given ration. For example, in a corn-soya broiler ration as much as 90% of the total ration may consist of corn and soyabean oil meal alone. With this type of ration there is an increased possibility of encountering deficiencies of trace minerals as compared with the situation some years ago when rations were composed of a much greater variety of natural feedstuffs such as oats, bran and wheat middlings. In the latter case there was a probability that the grains and grain by-products came from different areas and there was accordingly little likelihood of soil deficiencies in any particular area adversely influencing the mineral composition of the ration as a whole. In view of these considerations the fact that herring meals can be relied upon for a variety of trace minerals is of obvious nutritional importance. The mineral compositions of the first and last composite samples in the series are shown in Table VII. In addition to the major elements it will be seen that appreciable amounts of the minor elements are also present in the herring meal.

TABLE VII. Mineral analyses of six composite samples of B.C. whole herring meal.

	Production dates of composite samples		
Minerals	Nov. 23 to Nov. 30	Feb. 17 to Mar. 5	Average
Calcium (%)	2.04	2.13	2.09
Phosphorus (%)	2.10	2.14	2.12
Sodium (%)	0.536	0.520	0.528
Potassium (%)	1.16	1.12	1.14
Magnesium (%)	0.142	0.115	0.129
Sulphur (%)	0.394	0.350	0.372
Iron (%)	0.0150	0.0145	0.0148
Copper (ppm)	12.1	7.45	9.78
Manganese (ppm)	0.78	0.64	0.71
Zinc (ppm)	220.0	222.0	221.0
Iodine (ppm)	0.54	0.51	0.53
Cobalt (ppm)	0.066	0.043	0.055
Molybdenum (ppm)	7.03	6.60	6.82

FAT

The average level of ether-extractable fat in the meals was 7.9%. This value, of course, is not a constant figure, since the percentage of ether-extractable fat in herring meal gradually decreases upon storage as a result of decreasing solubility as the fat oxidizes and polymerizes. Had the meals been analyzed for their fat content immediately following manufacture, the values obtained would accordingly have been higher. A recent study (March *et al.*, 1961, 1962) of the nutritive value of herring meal fat has indicated that the fat in freshly prepared herring meal is well utilized. It was further shown that antioxidant treatment of herring meal retards the decline in solubility and biological availability of the fat which normally occurs during storage.

ACKNOWLEDGMENTS

Regular collection of herring meal samples at a number of large fishing reduction plants was organized by Mr G. Boothby, Canadian Fishing Company, and Mr D. Barbour of B.C. Packers Ltd., and others under their direction. Mr Boothby was responsible for pooling samples and submitting them for industrial analyses.

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OBITUARY

Donald Johnston Milne

Donald Johnston Milne

1916 — 1961

Doctor Donald Johnston Milne, Senior Scientist at the Nanaimo Biological Station of the Fisheries Research Board of Canada, died suddenly on December 13, 1961 in San Francisco where he was attending a meeting of the Pacific Marine Fisheries Commission as an official Canadian observer.

Dr Milne was born in Regina, Saskatchewan, on March 22, 1916. He received his elementary and high school education in Regina and entered the University of Saskatchewan in 1936. He graduated with a Bachelor of Arts degree with distinction in 1939 and received his Master of Arts degree in freshwater biology in 1941. During both his undergraduate and graduate work he was closely associated with the late Dr D. S. Rawson in the latter's classical studies of the lakes of Saskatchewan and Alberta. Dr Milne's M.A. thesis was concerned with the taxonomy, distribution and life history of the caddis flies of Waskesiu Lake, Saskatchewan. During the academic year 1941–42, he was appointed Philip Carpenter teaching fellow in zoology at McGill University in Montreal.

Dr Milne enlisted in the Royal Canadian Air Force as a Medical Associate on June 12, 1942. Until his discharge in June 1945, he participated in research programs in Halifax and in Toronto on the physiology of high altitude flying and on the design of survival equipment.

In 1943 Dr Milne married Violet MacLean. Mrs Milne, a son Kenneth and a daughter Heather, survive him.

On his release from the R.C.A.F. in June 1945, Dr Milne joined the staff of the Board's Biological Station in Nanaimo, British Columbia. From 1945 to 1948 he acted as one of Dr A. L. Pritchard's principal associates in the 5-year Skeena River Salmon Investigation. Dr Milne's particular responsibilities included analyses of the statistics of commercial and native food fisheries, conduct of extensive tagging programs to trace the pattern of salmon runs through the Skeena fishing area, and studies of Moricetown Falls as an obstruction to the passage of salmon. The results of his pioneering studies of the Skeena fisheries, summarized in a paper in the Board's *Journal* in 1955, provided the basis for much of present-day management of the salmon fisheries in this area. His findings on Moricetown Falls resulted in construction of extensive fishways to alleviate difficulties of passage of the important salmon runs to the Morice system.

In 1948 Dr Milne received his Ph.D. from McGill, submitting a thesis on the comparative growth and morphology of the Pacific salmons and steelhead trout.

Beginning in 1949, Dr Milne concentrated on studies of chinook and coho salmon. His ability to synthesize complex statistical information and his knowledge of the practical aspects of fishing gave him a broad and deep understanding of the complicated coastwide fishery for these species. He worked closely with all levels of the fishing industry and with those in the Department of Fisheries of Canada responsible for regulation of the fishery. His door was always open to the many commercial fishermen who sought information. His advice guided the Department of Fisheries of Canada in the application of minimum size limits and closed-season troll regulations. His report on the movements of chinook and coho salmon off the British Columbia coast (published as a Board *Bulletin* in 1957) is an important reference work for salmon workers everywhere along the west coast of North America.

Dr Milne served as the chief Canadian expert on chinook and coho salmon in the International Conferences on Coordination of Fisheries Regulations in 1957 and 1959, and in 1957 and 1958 organized the Canadian part of a highly successful international program to study the movements of coho at the entrance of Juan de Fuca Strait.

For many years he attended meetings of the Pacific Marine Fisheries Commission as an official Canadian observer. Here he earned the respect of United States salmon research workers for his breadth of knowledge.

Late in 1960, Dr Milne expanded his field of activities to include studies to determine the status of the stocks of all species of salmon along the British Columbia coast. At the time of his death he was completing a manuscript concerning the chinook and coho salmon fisheries of British Columbia. This work is being published as a Bulletin of the Fisheries Research Board of Canada.

Dr Milne played a key role in bringing biological information to bear on the practical problems of management of Canada's Pacific salmon fisheries. His quiet competence and capacity for accurate and pertinent assessment of data will be sorely missed.

NOTES

Systaltic Muscular Action of the Kidney Tubules of Flounder

A rather interesting observation was made on kidney explants of winter flounder (*Pseudopleuronectes americanus*) which may have a bearing on the function of the kidney *in vivo*. The kidney was removed from an anesthetized fish, placed in Medium 199 containing 50 units of penicillin/ml, 50 units of streptomycin/ml, and 25 units of mycostatin/ml, and cut with scissors into a number of explants roughly 2 mm square[1]. Approximately 50 explants were transferred to a plastic tissue culture flask along with 2 ml of Medium 199 containing 10% human serum, and the above concentrations of antibiotics. As the tissue was obtained from a poikilothermous donor the cultures were incubated at 5°C in air. The medium was renewed weekly and the tissues examined periodically at a temperature of 20°C.

Pulsation occurred in the tubules of all explants during the 3 weeks of periodic microscopic examination (see Fig. 1). The systaltic motion, a contraction followed by a relaxation of certain sections of the kidney tubules, was activated apparently by the change of the culture temperature from 5 to 20°C. The systaltic action of a tubule was not regular but occurred generally at intervals of 10 to 40 seconds. Also the contraction in any one section of a tubule was independent of any other. As a result of each tubule contraction, the fluid within the lumen was forced along the tubule, a phenomenon resembling peristalsis. At 20°C vigorous systaltic action of the tubules was maintained for at least one hour and could be reactivated by reincubation of the culture overnight at 5°C. Thus it would appear that the energy required for the contraction of the kidney tubules at 20°C is depleted rapidly by activity and regained by incubation at 5°C.

Fisheries Research Board of Canada
Technological Station, Halifax, N.S.

P. M. Townsley
M. A. Scott

Received for publication November 14, 1962.

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[1] Cappel, Medium 199 (Hank's base) pH 7.0 supplied by Becton, Dickinson and Company, Canada, Limited.

J. Fish. Res. Bd. Canada, **20**(1), 1963.
Printed in Canada.

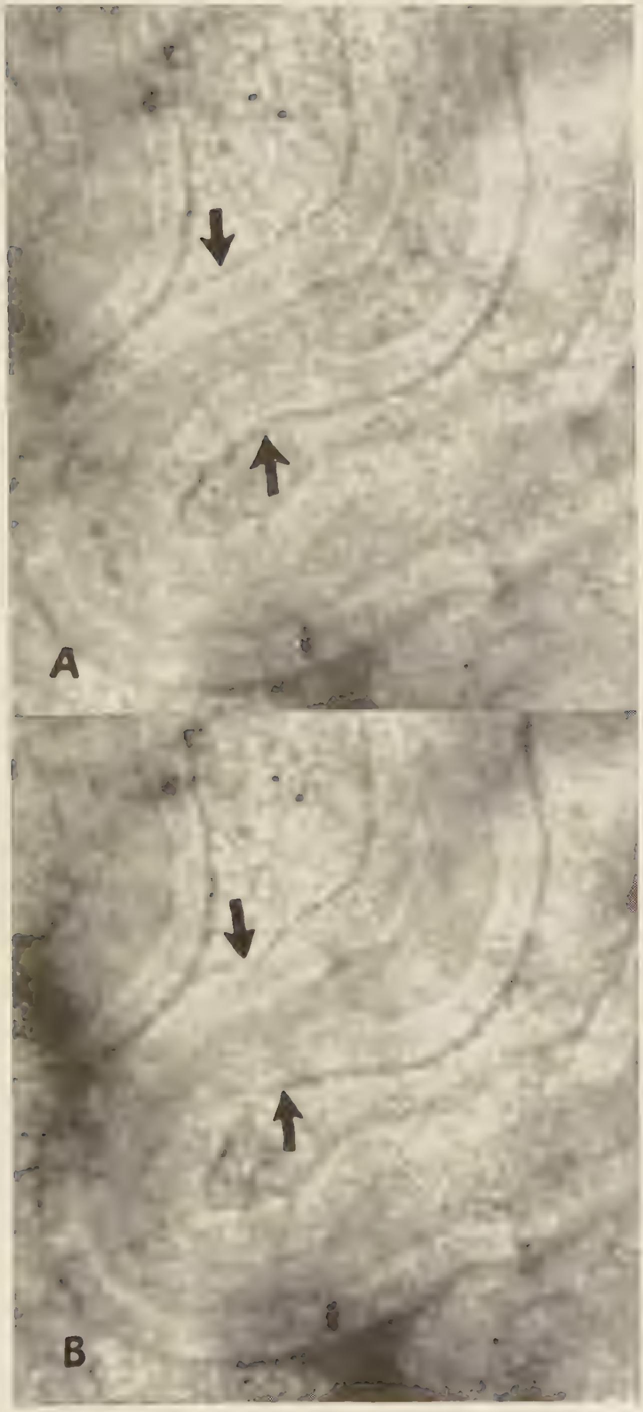

FIG. 1. Comparison of photographs A and B showing systaltic muscular action of a flounder kidney tubule in tissue culture (see arrows).

A Preliminary Investigation of the Blubber Oil from the Atlantic Bottlenose Whale

The Atlantic bottlenose whale, *Hyperoodon ampullatus* (Foster), a member of the family *Ziphiidae* or beaked whales, has been reported occasionally in eastern Canadian waters. Sergeant and Fisher (1957) list two documented captures, both about 22 feet long, but according to Pike (1956) the bottlenose whale grows to a length of 30 feet or more. Catches have been reported as far north as Frobisher Bay (Sergeant and Fisher, 1957), and also off Newfoundland, while a sizable industry exists in Norway. Catches of bottlenose whales reported from the Pacific coast probably all refer to Bairds Beaked whale, *Berardius bairdi.*

A Halifax, Nova Scotia, firm started exploratory whaling off the coast of Nova Scotia in 1962 using the schooner-type vessel *Minna.* In 3 trips to the waters near Sable Island, about 35 bottlenose whales were harpooned and some 60 tons of oil steam-rendered from the blubber. The identifications were made by two experienced Norwegian gunners. Since the oil from the bottlenose whale has been reported to be similar in composition to sperm whale oil (Bailey, 1952), a sample of this oil was obtained for analysis.

The analytical constants for the bottlenose whale oil (kindly supplied by the Karlsen Shipping Company, Limited, Halifax, N.S.), listed in Table I, were determined by the American Oil Chemists' Society Official Methods. For comparison, the values published for oils from bottlenose and sperm whales (Bailey, 1952), and Pacific bottlenose whale, *Berardius bairdi,* (Saiki, 1953) are reported. A sample of winterized sperm oil from Antarctica (kindly supplied by Marden-Wild of Canada, Limited, Halifax, N.S.) was also analyzed as a check on the analytical procedures.

Table I. Physical and chemical constants of whale oils studied.

Oil from	Source	Iodine value	Saponification value	Unsaponifiable matter	Refractive index	Triglycerides
			mg KOH/g	%	n_D^{25}	%
Bottlenose (*H. ampullatus*)	Karlsen	86.3	111.2	44.8	1.46268	7.5
Sperm, Antarctica	Marden-Wild	86.8	134.8	37.7	1.46316	–
Bottlenose	Bailey (1952)	79.7–88.7	121.5–135.9	35.0–43.2	–	–
Sperm	Bailey (1952)	70.4–96.4	120.0–150.3	17.5–44.0	–	26
Bottlenose (*B. bairdi*)	Saiki (1953)	87.4	123.2	40.05	$1.4560^{40°}$	–

J. Fish. Res. Bd. Canada, 20(1), 1963.
Printed in Canada.

In Table II the composition of the component fatty acids and fatty alcohols of oil from Atlantic bottlenose whale, *Hyperoodon ampullatus* (Foster), and of a commercial sperm oil as determined by gas–liquid chromatography is compared to values for sperm oils given by Hilditch (1956), Kovacs (1961) and Archer-Daniels-Midland (chart).

TABLE II. Gas–liquid chromatography area percent analysis of some component fatty acids and alcohols of whale oils as compared to values for sperm oil given in the literature.

	Component fatty acids			Component fatty alcohols		
	GLC area percent		Weight percent	GLC area percent		Weight percent
	Oil from: Bottlenose	Winterized Sperm	Sperm	Oil from: Bottlenose	Winterized Sperm	Sperm
Acid	Source: Karlsen	Antarctica Marden-Wild	Literature	Source: Karlsen	Antarctica Marden-Wild	Literature
10:0	–	1.2	1	–	–	–
12:0	Trace	4.0	1–7	–	–	–
12:1	–	–	1	–	–	–
14:0	4.0	7.2	5–10	2.4	4.6	2.1
14:1	1.4	2.9	4–6	–	–	–
16:0	3.9	10.1	6.5–14	19.0	30.0	21–25
16:1	16.1	21.8	16.7–26.5	7.6	8.4	7
18:0	1.1	1.2	0–2	5.3	4.4	1–5
18:1	26.7	28.7	28–37	46.2	45.5	49–66
20:1	29.0	8.7	8–19	15.1	4.6	6–8
20:5	–	0.9	–	–	–	–
22:1	14.0	2.4	3–4	1.0	–	–
Unknown	–	6.0	–	–	–	–
Others	3.8	4.9	–	3.4	2.5	–

The methyl esters were prepared from the fatty acids (freed of unsaponifiable matter) by the methanol–boron trifluoride method (Metcalfe and Schmitz, 1961) and the alcohols from the unsaponifiable matter were acetylated and determined according to Link *et al.* (1959). A Wilkens Aerograph model A–90 was used for the gas–liquid chromatographic analyses, operated with an oven temperature of 220° and carrier gas helium (inlet pressure 20 lb). The column of $\frac{1}{4}$ inch O.D. copper tubing was 10 feet in length, packed with DEGS polyester (25%) on 60–80 mesh GC-Super Support. Results are quoted as area percent since no standard correction factors were available.

The chief difference between bottlenose whale oil and sperm oil seems to be in the larger amounts of C_{20} and C_{22} monounsaturated acids and smaller amounts of short-chain C_{12} and C_{14} acids in the bottlenose oil. This difference is also reflected in the lower saponification value. However, the composition of the alcohols is very similar, the amount of the long-chain monounsaturated C_{20} alcohol being slightly higher in bottlenose oil. Saiki (1953) mentions that the blubber oil from the Pacific bottlenose whale, *Berardius bairdi*, contains C_{20} and C_{22} monounsaturated acids in particularly large amounts, but only 2% C_{20}

monounsaturated alcohol which is much lower than in the Atlantic bottlenose oil.

In general, however, the blubber oil from bottlenose whales is very similar in composition to the blubber oil from the sperm whale.

Fisheries Research Board of Canada
Technological Station, Halifax, N.S.

P. M. JANGAARD
R. D. BURGHER
R. G. ACKMAN

Received for publication November 20, 1962.

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Temperature and Rate of Hatching of *Triaenophorus* Eggs

On several occasions the eggs of *Triaenophorus crassus* and *T. nodulosus* were hatched at Heming Lake, Manitoba, and at London, Ontario, to obtain coracidia for experimental infections.

Preliminary attempts to rear *T. crassus* and *T. nodulosus* for coracidia were first made in 1953; details are available in a mimeographed Manuscript Report (No. 623) which is available at all stations of the Fisheries Research Board of Canada. The eggs were maintained at temperatures between 2 and 4°C. In this temperature range no hatching occurred for 20 days and most of the hatching took place between 25 and 35 days (Fig. 1).

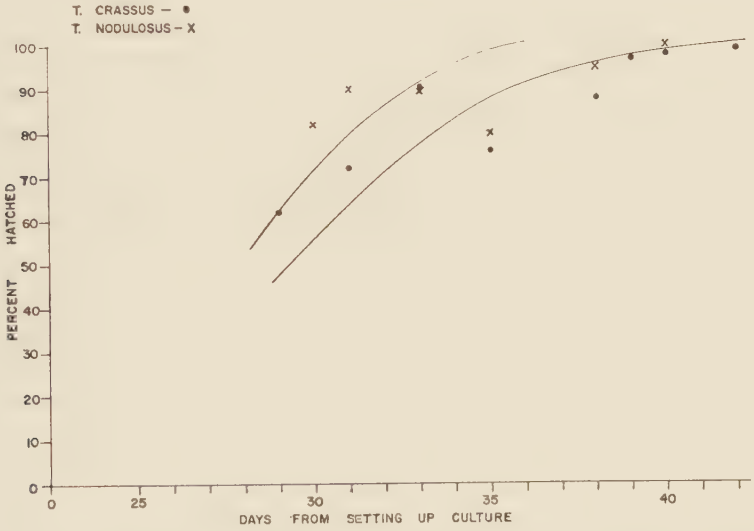

FIG. 1. Rate of hatching of *Triaenophorus crassus* and *T. nodulosus* eggs maintained at temperatures between 2 and 4°C.

In cultures maintained at room temperature (20–25°C), with and without constant aeration, hatching occurs in 4 to 10 days. Lack of aeration seems to depress the rate of hatching (Fig. 2). When the hatching data are plotted on the basis of day-degrees (C) of temperature accumulated, it is seen that hatching commences after 100 day-degrees and is practically finished following 400 day-degrees (Fig. 3 and 4). As might be expected, live coracidia are most plentiful in the cultures when about 50% of the eggs are hatched. There is some indication from infection experiments that coracidia hatched from cultures refrigerated for long periods of time may not be as capable of infection as coracidia hatched at slightly higher temperature, and thus at a faster rate of hatching.

J. FISH. RES. BD. CANADA, 20(1), 1963.
Printed in Canada.

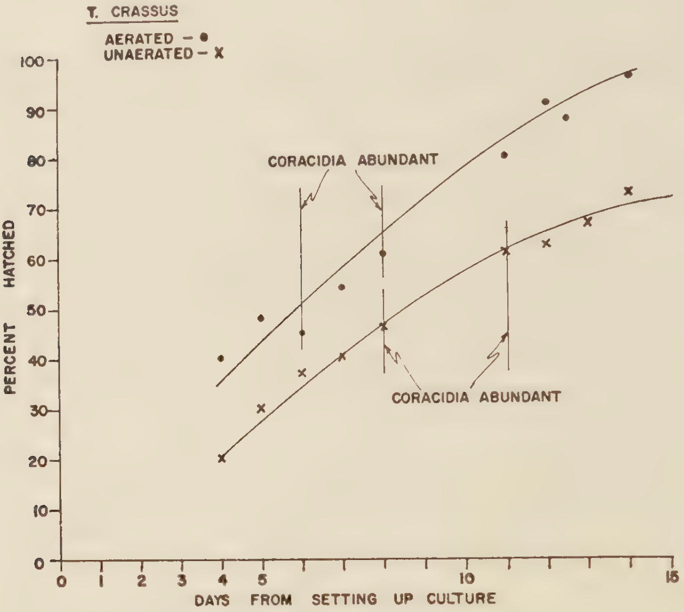

FIG. 2. Rate of hatching of aerated and non-aerated *Triaenophorus crassus* eggs held at temperatures between 20 and 25°C.

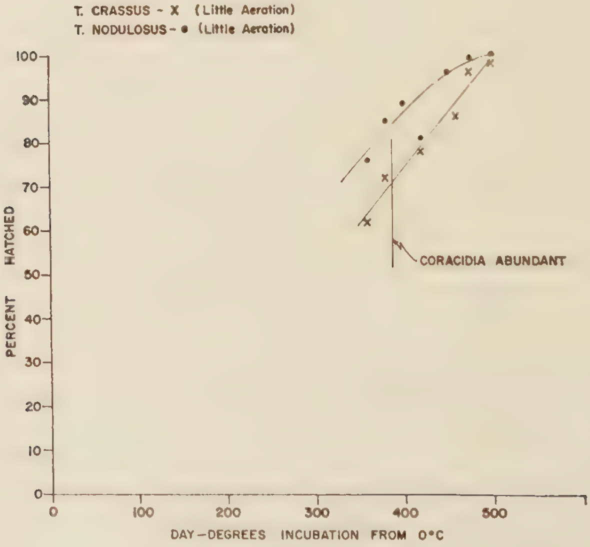

FIG. 3. Number of day-degrees above 0°C required to hatch slightly aerated eggs of *Triaenophorus crassus* and *T. nodulosus* incubated at Heming Lake in May 1953.

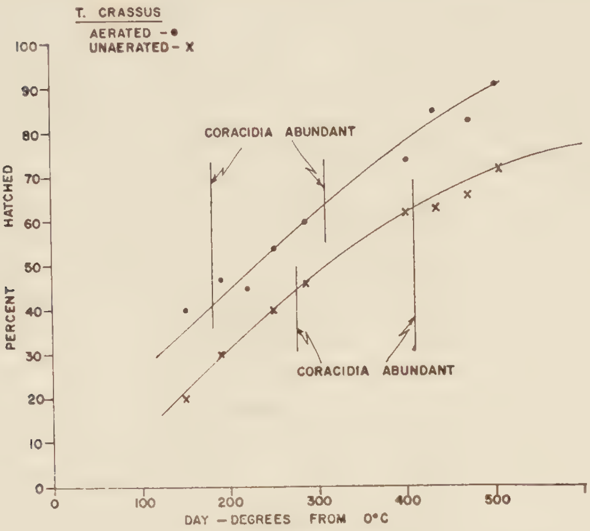

FIG. 4. Number of day-degrees above 0°C required to hatch aerated and non-aerated eggs of *Triaenophorus crassus.*

Guttowa (1958) describes the hatching rates, mortality and infectivity of eggs of *T. lucii* (Müll.) = *T. nodulosus*. The results reported herein are in general agreement with this more detailed experiment. Guttowa found no hatching below 2°C with eventual death of the embryo after 40 days. At 2–4°C about 50% of the eggs hatched in 15 days, and between 5 and 20°C complete hatching occurred in from 16 to 5 days. Eggs held at 2°C for increasing periods of time hatched rapidly when exposed to room temperature.

The general results appear to indicate that eggs can embryonate but not hatch below 2°C, and that they eventually use up their energy reserves or otherwise become non-viable as time progresses.

Under natural conditions the eggs of *T. crassus* and T. *nodulosus* are shed from the pike gut in early spring in shallow water. In Heming Lake the water temperature in such areas during this period is about 4°C. It would be expected then that under these conditions the eggs would hatch in about 15 days.

The authors wish to acknowledge the able assistance of Messrs A. B. McBurney and C. D. O. Foster in setting up and maintaining the egg cultures.

Fisheries Research Board of Canada
Biological Station
London, Ontario.

N. H. F. WATSON[1]
G. H. LAWLER

Received for publication October 12, 1962.

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[1] Present address: Laboratory of Parasitology, Department of Biology, Wayne State University, Detroit 2, Michigan, U.S.A.

Additional Note on the Oceanic Puffer *Lagocephalus lagocephalus* (L.)

Templeman (1962) described a specimen of *Lagocephalus lagocephalus* (L.) caught in Newfoundland as apparently the first of this species to be captured on the western side of the Atlantic. Recently, however, we have found in Fowler (1936) the description of a 505 mm individual of *L. lagocephalus* based on a dried specimen from Bermuda. I am grateful to Mr E. I. S. Rees of this Station for calling this reference to my attention.

Fisheries Research Board of Canada
Biological Station, St. John's, Nfld.
W. TEMPLEMAN

Received for publication November 30, 1962.

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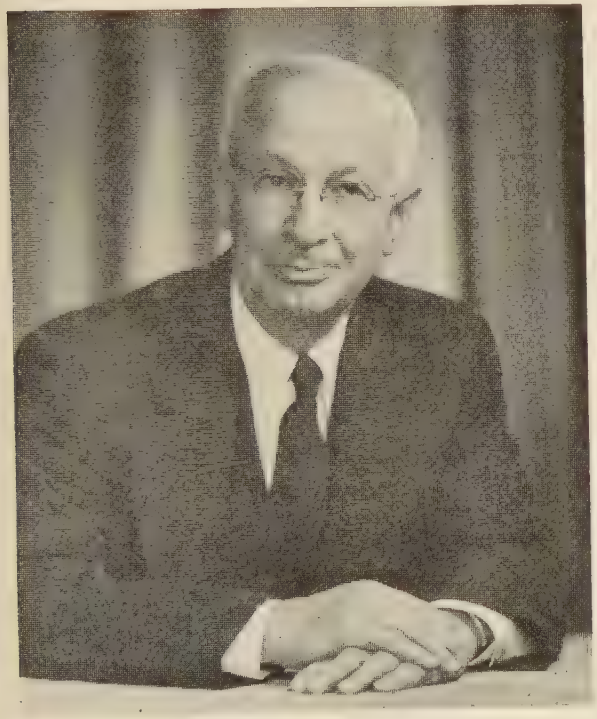
J. FISH. RES. BD. CANADA, **20**(1), 1963.
Printed in Canada.

J. R. DYMOND — An Appreciation

This issue of the Journal of the Fisheries Research Board of Canada is dedicated to an outstanding Canadian biologist, John Richardson Dymond, in recognition of his services to the Fisheries Research Board of Canada and to Canadian fisheries generally.

Dr. Dymond was born in Middlesex County, Ontario, October 4, 1887. He studied biology at the University of Toronto, and received the degree of Bachelor of Arts in 1912, together with the Victoria College Gold Medal in Natural Science. In 1920 he obtained the Master of Arts degree, also from Toronto, and in 1950 the Honorary degree of Doctor of Science from the University of British Columbia.



Ashley & Crippen, Toronto

Following six years as botanist with the Canada Department of Agriculture, Dr. Dymond became lecturer in the Department of Zoology at the University of Toronto in 1920 and rose to become Head of that Department in 1948. In addition, from 1922 to 1949 he was first the Secretary and later the Director of the Royal Ontario Museum of Zoology. Museum affairs were his major occupation during this period, but he also taught various University courses and took an active part in the field investigations of the Ontario Fisheries Research Laboratory. From 1948 to 1956 the cares of a department Head occupied most of his time. Since 1956 he has been engaged as a Consultant by the Ontario Department of Lands and Forests.

Always Dr. Dymond has stressed the need to bring biology to the citizen—partly so that biological considerations may play a just role in determining public policy, partly for the greater enjoyment of the world we live in. He has been active in numerous societies and associations that foster enthusiasm for biology and direct biological knowledge toward the wise and adequate use of living resources. These include The Brodie Club, the Canadian Conservation

J. Fish Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

Association, Conservation Council of Ontario, Federation of Ontario Naturalists (President, 1955–59), National Association of Audubon Societies, Ontario Federation of Anglers and Hunters, Ontario Society of Biologists (President, 1945–49), Toronto Anglers Association, and Toronto Field Naturalists Club (President, 1929–31).

Among government bodies, in addition to the Fisheries Research Board of Canada, Dr. Dymond has been a member of the Advisory Committee on Fisheries and Wildlife Research of the Ontario Research Foundation (Chairman, 1947 to date), he is member of an Advisory Committee to the Ontario Minister of Lands and Forests, and since 1960 he has represented the Ontario government as a member of the Great Lakes Fishery Commission.

In spite of this large volume of administrative and extra-mural activity, throughout his career Dr. Dymond has completed more than 50 scientific publications, mostly concerning fish, as well as an equal number of articles bringing the results of scientific work to a wide audience. He has been member of scientific societies such as the Ecological Society of America, the American Society of Ichthyologists and Herpetologists (President, 1940–42; Distinguished Fellow, 1961), and the Royal Canadian Institute (President, 1939–40 and 1956–57). He is a Fellow of the American Association for the Advancement of Science, and of the Royal Society of Canada (President of Section V, 1939–40 and 1956–57). A position of honour and responsibility which he occupied from 1939 to 1961 was that of member of the International Commission on Zoological Nomenclature.

Dr. Dymond's associations with the Fisheries Research Board of Canada begin in 1926. In that year, and again in 1928, he spent some months at the Nanaimo Biological Station, collecting and studying the fishes of British Columbia. One permanent result of this activity is the Board's Bulletin No. 32: "The Trout and Other Game Fishes of British Columbia". From 1938 to 1958 Dr. Dymond was a Member of the Fisheries Research Board. The first portion of this period was a time when every effort had to be made to keep a minimum research program going with very limited funds and manpower. At the same time certain unusual needs had to be met related to the war effort, particularly in oceanography and in a survey of the fishery resources of the arctic. In 1946 began the postwar period of expansion. Programs of biological investigation, in particular, had to be increased rapidly to keep pace with problems presented by the exploitation of new fish stocks and the increased utilization of old ones. As Vice-Chairman of the Board during 1947–53, Dr. Dymond had the final responsibility for approving the channels into which this increased biological research activity became directed.

It can be argued, however, that Dr. Dymond's greatest contribution to the Fisheries Research Board of Canada and to the fisheries of Canada consists of the numerous young people whom he influenced and stimulated while they were students at Toronto. About 40 present members of the Board's staff have had this contact, whether as Major Professor, Department Head, or simply as counsellor and friend. The papers in this issue of the Journal are written by some of these scientists, and are respectfully dedicated to their friend "J.R."

Big Effects from Small Causes: Two Examples from Fish Population Dynamics[1]

By W. E. Ricker

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

1. A population which, before exploitation, includes upwards of 12–15 age-groups in appreciable quantities, is very sensitive to fishing. For example, even as little as 5% catch per annum eventually causes a major reduction in the relative weight of older fish in the stock. With unchanging recruitment the absolute size of the total stock also declines markedly, or even catastrophically, under moderate exploitation—so much so that it seems likely that recruitment must usually increase when the stock is first thinned, partly compensating for the removals.

2. A population that produces its greatest sustained yield at a high rate of exploitation—say 75% or more at average recruitment—is then close to a point where recruitment will fall off rapidly if utilization becomes only slightly more intensive. This fact, and the aggravating effect of environmentally-caused variations in recruitment, suggest that any really close approach to the point of optimum yield will usually be too dangerous to be practical.

INTRODUCTION

In 1928 Professor J. R. Dymond initiated the writer into the cult of those who apply quantitative methods in the broad science of ichthyology. In the loft of Lou Joyce's fish house at Port Credit, Ontario, he set me the task of measuring and computing body proportions of some scores of fourhorn sculpins, then called *Triglopsis thompsoni*. This was a congenial occupation, partly because I was keen to put to practical use the slide-rule know-how recently acquired in Professor John Satterly's first-year physics course—well remembered by several generations of University of Toronto students.

This early experience with fish morphometry led eventually and by circuitous routes to the realm of fish population dynamics. Exploratory excursions with slide-rule and calculator, made in the latter region over the past 10 years or so, have turned up numerous odd bits of information in addition to some that did contribute to the current objective. Most of these unassorted conclusions are not of much general interest. A few, however, seem likely to shed light on events or problems in the known history of fish populations, or in their future prospects.

Two relationships of the latter type are presented herewith. The general background of the models and computations used, as well as the symbols employed, are as given in several earlier papers [2], [3] and [4].

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[1] Received for publication October 29, 1962.

J. Fish. Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

EFFECT OF DIFFERENT RATES OF FISHING ON POPULATION STRUCTURE

In the year of the armistice, 1918, A. G. Huntsman and F. I. Baranov independently called attention to the *molozhenie* or juvenescence of a fish population that occurs when a fishery is introduced. Since then several additional models have been published to illustrate this phenomenon (references in [3]), and it has often been observed in nature. However, no one seems to have made a systematic examination of the quantitative effects of different levels of fishing on a population. Thus it is logical to compute and compare, even if somewhat belatedly, the effects of a graded series of different rates of fishing on the weight of a fish stock.

Weight rather than numbers has been chosen for illustration here, because the weight of a stock is of more direct commercial interest, and it is also more directly related to reproductive potential. Changes in numerical abundance of a stock resulting from increased fishing are similar to but less extreme than the changes in weight.

In the population model examined, recruitment at age 1 is held at a constant level. The growth rates and natural mortality rates used (Table I) are essentially those quoted by Chatwin [1] for a population of lingcod (*Ophiodon elongatus*). The exact figures of course make little difference here; this range of natural mortality rates is of the right order for a number of other important stocks of marine fishes—for example, cod and redfish off the Atlantic coast of Canada—except that the increase in mortality rate among the oldest fish is probably too abrupt.

TABLE I. Growth rates, natural mortality rates, and average weight of the fish of the stock of Fig. 1. Fish weights are shown for the start of each year indicated. Based on the estimates for lingcod in tables 7 and 8 of Chatwin (1958); values beyond age 16 are extrapolated.

Year of life	Weight (*kg*)	Instantaneous rates		Year of life	Weight (*kg*)	Instantaneous rates	
		Growth	Mortality			Growth	Mortality
1–2	0.17	1.56	0.35	11–12	8.3	0.09	0.30
2–3	0.81	0.66	0.30	12–13	9.1	0.08	0.35
3–4	1.56	0.40	0.25	13–14	9.8	0.07	0.40
4–5	2.33	0.29	0.20	14–15	10.6	0.06	0.50
5–6	3.12	0.24	0.20	15–16	11.2	0.05	0.60
6–7	3.96	0.20	0.20	16–17	11.8	0.04	0.80
7–8	4.94	0.16	0.20	17–18	12.3	0.03	1.10
8–9	5.8	0.14	0.20	18–19	12.6	0.02	1.50
9–10	6.7	0.12	0.20	19–20	12.9	0.02	2.20
10–11	7.5	0.10	0.25	20–21	13.2	. . .	. . .

Figure 1 shows the age structure of the unexploited population in terms of weight, and also its equilibrium structure at several rates of fishing. The latter figures also represent the age structure of the catch quite well, and will do so exactly if fishing occurs during a short period of time each year, before natural mortality or recruitment begin to operate.

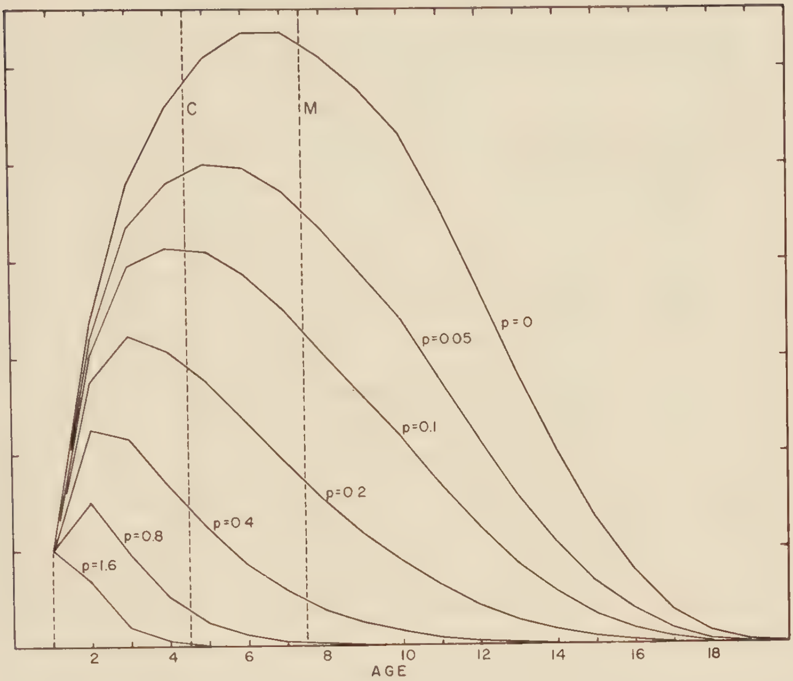

FIG. 1. Weight of the fish present at successive ages, for different rates of fishing (p), in terms of a unit weight of recruits at age 1, for the population of Table I. With constant recruitment, the equilibrium weight of the stock is proportional to the area under each shell. C: average minimum age limit of usable fish; M: average age of first maturity.

What strikes the eye in Fig. 1 is the tremendous effect that even a little bit of fishing has, on the total bulk of the stock, and (still more) on its distribution by age. A 10% per annum fishery, for example, reduces the weight of the stock to little more than half of the original; while 33% utilization, which is not usually considered excessive, reduces its bulk to 16% of the original (Table II).

If the smaller fish are not marketable, yet are unavoidably caught (and are discarded dead), the reduction in *usable* stock is even greater. Though it doesn't actually apply to lingcod, a cull limit between ages 4 and 5 is indicated by line C in Fig. 1, and its effect is examined in column 4 of Table II. The size of the usable stock is reduced well past 50% by a 10% fishery, and it is down to 7% when exploitation reaches 33%.

Finally, the weight of the *mature* stock is of interest, since this represents the reproduction potential. In lingcod first maturity for females is mostly at age 7 or 8 (Fig. 1, line M), and column 5 of Table I shows the weight of all fish older than 7. In this case a 10% fishery reduces the spawners to 38% of their original bulk, while 33% annual removal gets them down below 3%. At 55% utilization, which is by no means impossibly large, the bulk of the spawners is reduced to $\frac{1}{850}$ of the original.

TABLE II. Relative weight of stock for each of the equilibrium populations of Fig. 1, and for two age ranges within those populations.

1	2	3	4	5	6
		Relative weight of stock			
Rate of fishing p	Rate of exploitation u	Total (All ages)	"Usable" (Ages 5–20)	Mature (Ages 8–20)	"Usable" catch per unit effort
0.	0.	100.	100.	100.	100.[a]
0.05	4.9%	72.7	67.6	61.7	66.0
0.10	9.5%	54.5	46.6	38.6	44.4
0.20	18.1%	33.3	23.4	15.6	21.2
0.40	33.0%	16.1	6.95	2.80	5.73
0.80	55.1%	6.68	0.883	0.117	0.608
1.60	79.8%	2.91	0.025	0.0003	0.012

[a]This applies to a vanishingly small rate of fishing.

It is obvious that these effects result from the cumulative action of individually-small percentage removals, operating throughout many years of the life of these fish: it is compound interest in reverse. If a fish species is naturally shorter-lived than the one used here (i.e., has larger natural mortality rates somewhere within the range of ages shown in Table I), then the effects of fishing on stock density are less spectacular. Contrariwise, there are a number of species with considerably smaller natural mortality rates than those used here—to judge from the very old specimens that were formerly rather common, and are still caught occasionally, among halibut, *Hippoglossoides*, etc. For these species the effects of a small rate of utilization will be even more startling than those shown in Fig. 1.

DECLINE IN CATCH PER UNIT OF FISHING EFFORT

With recruitment still maintained at a steady level, column 6 of Table II shows approximately the decrease in usable catch, per unit of fishing effort, that occurs as fishing effort is increased.[2] The decline in fishing success is large even at low fishing intensities: a mere 5% per annum fishery eventually reduces catch per hour by 34%, while the 33% fishery reduces fishing success to less than 6% of the original.

How can a moderately intensive fishery survive, in the face of so great a decline in revenue? The answer is that most of them could not survive, but in practice catch per hour does not usually fall so low. In some cases, though not in all, the rate of growth of the individual fish increases somewhat, partly compensating for reduced abundance. What is most likely to have happened generally, however, is that the (absolute) annual recruitment has increased as a result of the major thinning of the stock that occurs at quite an early stage of exploitation. This phenomenon has not been documented by direct estimates of recruitment made as rate of fishing increases, but I believe this is because for most fisheries the increase in recruitment is largely completed during the early stages of their development, when few or no biological observations were being made on the stock. By the time the rate of exploitation has become no more than 9–10% per year, the stock of Fig. 1 has already been reduced to about half its original bulk, and the spawners to much less than half (Table I). By this time a population will usually have reached a plateau on its graph of recruitment against stock size, or be near the top of a dome. Hence observations made from that time onward will not detect any negative slope in the relation of recruitment to parental stock. Nevertheless the general quantitative aspects of the situation often suggest strongly (for naturally long-lived fish) that there must have been a substantial increase in average annual recruitment during the time of the initial thinning of the stock, while the fishery was still young.

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[2] Column 6 of Table II is computed on the basis that effort is proportional to rate of fishing, p, where $p = -\log_e (1 - m)$. The "conditional" rate of fishing, m, is the same as the rate of utilization or exploitation, u, in the situation where all the catch is made early in the statistical year, before natural mortality operates. This is the u shown in column 2 of Table II, so that column 6 of that Table is equal to column 4 multiplied by column 2 and divided by column 1. If however natural and fishing mortality operate concurrently to some extent, the true rates of exploitation would be progressively somewhat less than those shown in column 2, and the catch per unit effort would decline somewhat more rapidly than the series of figures in column 6. With complete overlap of times of fishing and natural mortality, at $p = 0.8$ the catch per unit effort is about two-thirds of what is shown in Table II.

EFFECT OF HEAVY FISHING ON RECRUITMENT TO A POPULATION

In the absence of positive information, estimates of the role of stock abundance in governing recruitment to a population have usually varied between the assumption of direct proportionality and that of effective independence. It is recognized that neither extreme can be applicable over the whole range of possible stock sizes: unlimited direct proportionality would increase a population without limit, while complete independence implies that recruits can be obtained from no spawners at all. In recent years observations on the actual or relative magnitude of recruitments have become available, and there are now a number of oceanic fish stocks for which recruitment has not been demonstrated to have any trend upward or downward over quite a wide range of spawning stock sizes. As a result there is a tendency to use independence as the norm in discussing the dynamics of exploited marine fishes. Even if an early phase of negative slope occurs, as was postulated in the previous section, it is no longer accessible to observation and it is unlikely to reappear as long as fishing continues at a moderate, or even rather low, level of activity.

No one, of course, goes to the extreme of obtaining progeny from no parents. This means that there must be an initial rapid rise in recruitment at stock levels close to zero.

Thus a common picture of the average relationship between stock and recruits among sea fishes is of the type shown by the solid line in Fig. 2. Figure 3 is the curve of equilibrium catches taken from this average recruitment, as rate of fishing is increased. The long slowly-ascending portion shows the increase in catch as rate of fishing is increased from zero to its best value. The steep right-hand portion is the rapid decline that follows when exploitation exceeds this level.

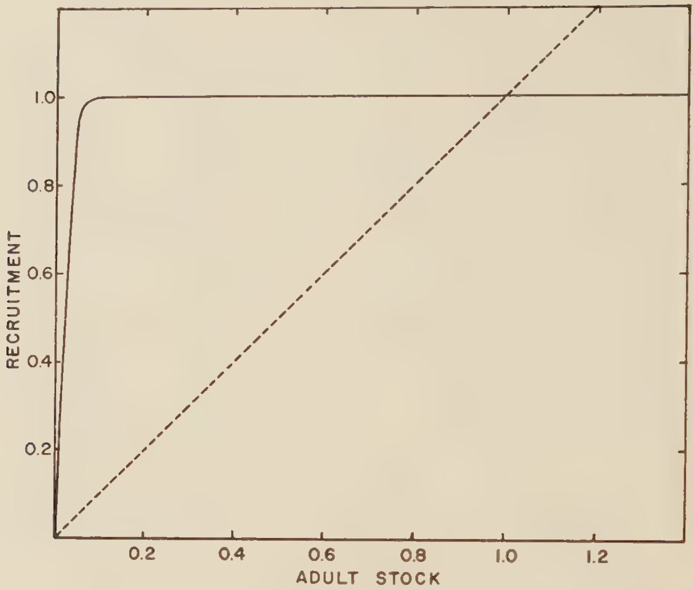

FIG. 2. A recruitment curve of the type where recruitment is independent of spawning stock density over most of the range of the latter. In this example, R = 1 between W = 0.1 and W = 1; R/W = exp[3.153(1–W)] between W = 0 and W = 0.05, which makes a slightly curved ascending line; the short transition interval between W = 0.05 and W = 0.1 is sketched in freehand.

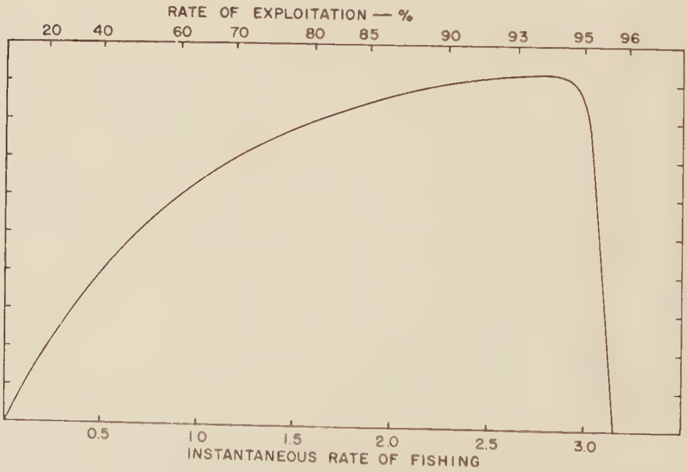

FIG. 3. Relative size of catches obtained from the population of Fig. 2, as fishing effort is increased (assuming all fishing is at one age, or that growth just balances natural mortality in later years). The rate of exploitation (u — top scale) is the fraction of the total recruitment (Fig. 2) taken by the fishery at equilibrium. The rate of fishing (p — lower scale) in most fisheries would be approximately proportional to the fishing effort necessary to take the catch indicated.

The rapidity of this decline, and dangers associated with it, seem to have escaped special comment. In the example used, an increase from 94 to 96% utilization spans the change from maximum yield to no yield at all. Assuming fishing effort is proportional to rate of fishing, this means an increase in effort from 2.8 to 3.2, or by only 14%. If the ascending limb of the reproduction curve of Fig. 2 be made straight, the descending limb of Fig. 3 becomes completely vertical; in which event only a knife-edge separates full utilization from complete collapse of the fishery[3].

There are buffering factors of course. Figure 3 represents *equilibrium* conditions, which (on the ascending limb of the Fig. 2 curve) are reached asymptotically rather than immediately, following any increase in fishing mortality to a new steady level. Also, when more than one age of the fish contributes importantly to the fishable stock (which can be consistent with a high rate of exploitation if recruitment to the fishable stock occurs during more than one year of life), a collapse of reproduction in just one season would not be immediately fatal. Nevertheless, if ever the rate of exploitation exceeds the optimum for a short series of years, even if only slightly, the decline in stock and catch will evidently be swift and drastic.

This conclusion is not restricted to stocks characterized by flat-topped reproduction curves. It obviously must apply to any population where best yield is obtained from a small spawning stock: that is, where optimum rate of exploitation is large—say 75% or more. Indeed for any population "obtaining maximum yield will always be a bit tricky—with a more drastic penalty for too much fishing than for too little"[3].

If reproduction of a population adhered closely to average conditions, precise regulation of the fishery on these stocks would naturally be much easier. In practice, the recruitments that determine a curve such as that of Fig. 2 may easily vary by a distance of up to say 0.9 on either side of it. This means that no single optimum rate of utilization will be applicable every year. But there is a difference in the room for manoeuvre on either side of the norm. In years of better than average stocks, rate of utilization need be increased only slightly over the best level for average recruitment, since the latter rate is already quite close to 100% (it is 94% in Fig. 3). In years of poor stocks, on the other hand, rate of utilization will have to be reduced more substantially in order to maintain a spawning stock close to the optimum. For example, if recruitment "accidentally" fell to 0.1 in Fig. 3, the fishery should not take more than 50% if the stock is to stay out of the region below 0.05 where reproduction becomes disastrously low.

The argument is sometimes heard, concerning stocks whose average reproduction is of the type described by Fig. 2, that because environmental variability causes such great variation in recruitment, there is no need to worry about the size of the spawning stock. This will be true as long as the stock remains well away from the "breaking point" of reproduction, at the left end of the recruitment curve. But for maximum utilization the fishery for such a population must be adjusted with the greatest care to the size of the stock present each year. If this is not possible, utilization at considerably less than the maximum rate is the only way to ensure the continued existence of a good stock and a productive fishery.

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[3] On page 244 of [2] there is a yield diagram for a flat-topped reproduction curve with a less abrupt increasing phase: the broken curve plus the B curve to the right of it represents the catch. In this case the optimum rate of fishing was 1.58, corresponding to 79% catch each year.

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Growth and Mortality of Whitefish in Three Unexploited Lakes in Northern Canada[1]

By W. A. Kennedy

Fisheries Research Board of Canada
Biological Station, London, Ont.

ABSTRACT

Whitefish (*Coregonus clupeaformis*) ages were determined for small samples from Nueltin, MacDonald and MacEwen Lakes, N.W.T., Canada. Growth rate was comparatively fast in MacEwen Lake, intermediate in the others. Natural annual mortality rates of 57, 81 and 74% respectively were derived.

INTRODUCTION

The stimulus for this study was Ricker's statement (1949) that, "Studies of unexploited populations are prized rarities in fishery literature." There are many unexploited lakes in the Northwest Territories of Canada, and several that have been exploited for the first time since Ricker's paper appeared. From three of these, namely, Nueltin, MacDonald and MacEwen Lakes, samples of whitefish, *Coregonus clupeaformis*, were taken before the populations were exploited appreciably.

MATERIALS AND METHODS

Instructions given to the samplers were designed to provide representative samples. From each fish in a sample a number of scales were taken from an area just above the lateral line and under the dorsal fin. Data on time and place of capture and on the weight of each fish were recorded on the individual coin envelope in which the scales from that fish were stored. At a later date, magnified images of the scales were examined at the Biological Station, London, and ages were determined from them by standard methods. All age determinations were made by Mrs B. M. Johnson, an experienced scale reader. The data concerning each fish were recorded on an IBM punch card; the cards were used to derive Tables I, II, III and IV.

Pertinent particulars about the three lakes and on sampling at each are as follows:

Nueltin Lake is at 100° W longitude, about 80% of its area lying in the Northwest Territories, the remainder in Manitoba. It is approximately 1000 square miles (260,000 hectares) in area exclusive of islands, and its drainage basin, mainly Precambrian granite, is about 12,000 square miles (31,000,000 hectares). It lies just south of the northern limit of trees and is drained to Hudson Bay by the Thlewiaza River. The water is reported to be clear, ice-covered until July, and to have many shoals. Mr F. W. Mowat (personal

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[1] Received for publication August 15, 1962.

J. Fish. Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

communication) found a maximum depth of 150 feet (45 metres) on the basis of very few soundings. Harper (1948) found eleven species of fish in the lake.

Between September 14 and 22, 1948, Mr A. H. Lawrie, a biologist then engaged in research on caribou, collected scales from 24 whitefish. These were sent to Dr W. B. Scott, of the Royal Ontario Museum of Zoology in Toronto, who has made them available for this study. Between August 14 and 26, 1949, Mr Lawrie, as a favor to the author, collected scales from an additional 64 whitefish. Mr Lawrie sampled all the fish taken in four-inch-mesh (10-cm) stretched measure gill nets set at the mouth of Windy Bay, near the north end. Mr F. O. Martin, who wanted a permit to fish the lake commercially, forwarded 24 whitefish in ice to the author for examination and scales were taken from them on November 14, 1949. Mr Martin also sent 166 fresh whitefish to officers of the Department of Fisheries of Canada who secured scales at an unspecified date in December 1949. Mr Martin reports that both lots of fish were taken from the south end. They were taken by two unnamed commercial fishermen using gill nets whose mesh is unknown, but probably about five-inch (13-cm). Because the fishermen were untrained in sampling and received any instructions on sampling through intermediaries, it would be legitimate to question whether they supplied representative subsamples.

MacDonald Lake lies just north of 62° N latitude and just west of 111° W longitude. It is southeast of, and near, Great Slave Lake into which it drains. Planimeter measurements on a recent map indicate that its area is 32 square miles (8,300 hectares). Although it is within the Canadian Shield, geological maps indicate a basin of sedimentary rock. The water is very clear and the lake is at least 390 ft (120 m) deep. The bottom is sand, gravel and rock.

The lake was fished commercially for the first time in early 1953 by fishermen based at Hay River on Great Slave Lake. Mr R. Wheaton, the biologist then responsible for sampling the commercial catch on Great Slave Lake, took scales from 50 MacDonald Lake whitefish on January 27, 1953 and 196 more on February 23, 1953. The sample was designed to be representative of whitefish catches in the $5\frac{1}{2}$-inch-mesh (14-cm) gill nets used by the commercial fishery while the population was still essentially unchanged by exploitation.

MacEwen Lake is roughly 6 miles (10 km) long and nowhere more than one-half mile (0.8 km) wide. Its long axis lies approximately southeast–northwest and intersects longitude 120° W at about 60° 50′ N latitude. The lake was named informally after an officer of the Department of Fisheries of Canada and the name may not be officially recognized. Planimeter measurements on a recent map indicate that its area is 1.7 square miles (440 hectares). It lies outside the Canadian Shield at an altitude of approximately 1000 ft (300 m) and drains to Mackenzie River by Trout River. The maximum depth recorded is 50 ft (15 m). The water is clear, brownish and tastes slightly of sulphur. The bottom is a soft mixture of sand and mud.

The lake was fished commercially for the first time in early 1960 by fishermen based at Hay River on Great Slave Lake. Messrs K. Roberts and C. Haight, technicians thoroughly trained to sample the commercial catch on Great Slave

Lake, took scale samples from 198 MacEwen Lake whitefish on March 18, 1960 and from 80 on April 1, 1960. The sample was designed to be representative of whitefish catches in the 5½-inch-mesh (14-cm) gill nets used by the commercial fishery while the population was still essentially unchanged by exploitation.

RELATIONSHIP BETWEEN AGE AND WEIGHT

The relationship between weight and age is given in Tables I, II and III for Nueltin, MacDonald and MacEwen Lakes respectively. Weights are grouped to the nearest half pound; in some cases the weights were originally taken in ounces, in other cases in tenths of pounds. Ages are given in terms of number of annuli counted; in every case there were several circuli outside the outermost annulus. Three of the 267 lots of scales in the sample from Nueltin Lake consisted entirely of regenerated scales from which ages could not be determined, so they contribute nothing to Table I. Weight had not been recorded in the case of three others, all 12-year-olds. Therefore, a total of 261 fish are involved in the weight distributions and average ages of Table I, and ages were determined for a total of 264. Eighteen of the 246 lots of scales from MacDonald Lake consisted of regenerated scales, as did three of the 278 lots of scales from MacEwen Lake.

Tables I, II and III illustrate that in each of the three lakes whitefish of a given age vary greatly in size and that whitefish of a given size vary greatly in age. They also give some indication of the effect of net selection. It seems reasonable to expect commercial gill nets to catch various sizes of large whitefish

TABLE I. The number of whitefish of a given age which are of a given weight in a sample taken from Nueltin Lake, N.W.T., in 1948 and 1949. Weights recorded originally partly in ounces, partly in tenths of pounds, here grouped to the nearest half pound (1 pound = 0.3732 kilogram).

Weight (lbs)	Age (i.e. number of annuli)								
	8	9	10	11	12	13	14	15	16
1½	3	...	...	...	...	...	...	...	...
2	0	1	1	1	1	...	...	...	...
2½	1	2	1	2	3	...	...	...	...
3	...	1	4	3	7	4	...	1	...
3½	...	0	10	12	7	6	...	...	...
4	...	3	9	20	16	12	1	4	...
4½	...	...	8	9	20	12	2	2	...
5	...	...	1	7	19	10	8	3	2
5½	...	...	...	...	4	3	6	1	0
6	...	...	...	...	...	2	3	0	1
6½	...	...	...	...	...	...	1	0	...
7	...	...	...	...	...	...	...	1	...
Av. Wt.	1.7	3.1	3.7	3.9	4.2	4.4	5.2	4.6	5.3
Total Number	4	7	34	54	80[a]	49	21	12	3

[a] Includes 3 fish for which age was determined but weight was not recorded.

TABLE II. The number of whitefish of a given age which are of a given weight in a sample taken from MacDonald Lake, N.W.T., in 1953. Weights recorded originally in ounces, here grouped to the nearest half pound.

Weight (lbs)	Age (i.e. number of annuli)							
	7	8	9	10	11	12	13	14
1½	1	...	...	...	...	...	...	...
2	...	...	1	2	...	...	...	...
2½	...	3	25	16	4	...	...	...
3	...	...	8	48	22	1	...	...
3½	...	...	2	23	28	12	1	...
4	...	...	...	3	12	10	2	...
4½	...	...	...	...	2	1	...	...
5	...	...	...	...	...	...	...	1
Av. Wt.	...	2.3	2.6	3.0	3.4	3.7	3.8	...
Total Number	1	3	36	92	68	24	3	1

TABLE III. The number of whitefish of a given age which are of a given weight in a sample taken from MacEwen Lake, N.W.T., in 1960. Weights recorded originally in ounces, here grouped to the nearest half pound.

Weight (lbs)	Age (i.e. number of annuli)							
	4	5	6	7	8	9	10	14
1½	1	...	...	...	...	...	...	...
2	3	3	...	...	...	...	...	...
2½	3	1	2	...	...	...	...	...
3	1	4	3	3	...	...	...	...
3½	1	5	11	4	...	...	...	...
4	...	3	19	5	...	...	...	...
4½	...	1	3	9	2	...	...	...
5	...	1	10	21	14	...	...	...
5½	...	...	5	24	8	2	...	...
6	...	...	4	26	13	0	...	...
6½	...	...	1	11	16	4	...	...
7	...	...	...	2	6	5	2	...
7½	...	...	...	...	2	1	1	1
8	...	...	...	...	3	3	0	...
8½	...	...	...	...	...	0	0	...
9	...	...	...	...	...	1	1	...
Av. Wt.	2.4	3.3	4.3	5.4	6.0	7.0	7.6	...
Total Number	9	18	58	105	64	16	4	1

in about the same proportion that they occur in any population, but to catch a much smaller proportion of small whitefish. The size distributions at given ages in the right-hand half of each of Tables I, II and III may therefore be regarded as approximately proportional to the size distribution in the lake. However, the further to the left a column lies in these tables, the more do size distributions in that column become truncated because of the failure of gill nets to catch the smaller fish of a given age in the same proportion as the larger fish. This net selection obviously affects the results least where rate of growth is fastest.

The advisability of combining the subsamples from Nueltin might be questioned, since two different mesh sizes were used. Also, the reliability of that part of the Nueltin samples taken by untrained samplers might be questioned. Table IV, which shows the distribution of ages within each of the four subsamples from Nueltin Lake, is a useful guide to consideration of these objections. Subsamples A and B are from the 4-inch-mesh, subsamples C and D from the larger mesh. Since age distributions in C and D tend to be intermediate between those of A and B, differences in mesh size seem of minor importance in this case. Also, since the two subsamples A and B which were taken by a trained sampler differed from one another by more than either differed from C or D, there is not basis for regarding the subsamples taken by these untrained samplers as less representative than those usually taken by trained samplers.

TABLE IV. Number of fish of each age in the four subsamples of whitefish which constitute the sample from Nueltin Lake

Subsample taken	Designation	Age (i.e. number of annuli)								
		8	9	10	11	12	13	14	15	16
Sept. 1948	A	3	1	3	1	5	9	2	0	0
Aug. 1949	B	0	0	0	13	19	19	4	7	2
Nov. 1949	C	0	0	1	2	6	1	1	1	0
Dec. 1949	D	1	6	30	38	50	20	14	4	1
Total:		4	7	34	54	80	49	21	12	3

GROWTH RATE

The average weight at each age is shown at the bottom of Tables I, II and III. The relationship is also shown graphically in Fig. 1. In Great Slave Lake (Kennedy, 1953) whitefish grow only during the period June to September, mainly during July and August. It is reasonable to expect that the growing season is much the same in Nueltin, MacDonald and MacEwen Lakes, since they are all at approximately the same latitude. If this is true, then the fish from MacDonald Lake, taken in January and February, and those from MacEwen Lake, taken in March and April, must in each case have made a full year's growth since the outermost annulus counted was laid down. In other

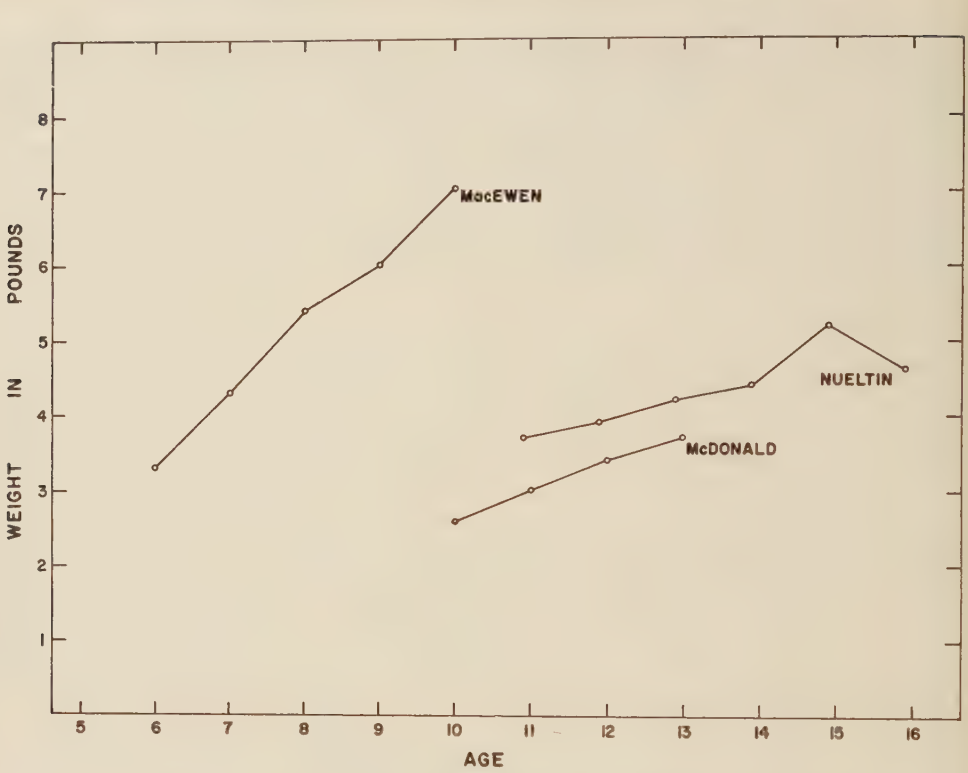

FIG. 1. Relationship between "age" and weight of whitefish in three Northwest Territories lakes. "Age" indicates number of growing seasons—see text.

words, a fish of age n in these samples has *completed* n + 1 growing seasons. Figure 1 indicates that average size is plotted against "age"; strictly speaking, average size is plotted against number of growing seasons completed.

Although most of the Nueltin Lake whitefish were taken in November and December, hence presumably had also finished growing for the year, some were taken in the last half of August and in September. Thus, on the average, fish in this sample had completed slightly less than a full year's growth since the outside annulus was laid down. If the seasonal growth pattern were exactly the same as in Great Slave Lake, then whitefish in this sample would, on the average, have completed 92% of the total growth expected during the year of capture. For the purpose of plotting these Nueltin Lake data on Fig. 1, it is assumed that average weights represent fish which on the average have completed n + 0.9 growing seasons, where n is the number of annuli.

If fish of a given size appeared in the sample in the same proportion as they occur in the lake population, then the curves in Fig. 1 would be growth curves for whitefish in the respective lakes, assuming growth rate to remain constant from year to year. Unfortunately, because of net selection, the younger fish caught are biggest for their age. The younger the fish the greater is the discrepancy. Therefore, the average weights of the younger fish in the sample are greater than the average weights in the population, the discrepancy being greater the younger the fish. Nevertheless, the curves in Fig. 1 are probably reasonable approximations to growth curves of whitefish in the respective lakes, particularly if the lower third of each is disregarded.

Figure 1 indicates the slowest growth in MacDonald Lake, a slightly faster rate in Nueltin Lake and a remarkably fast rate in MacEwen Lake. The growth rate in MacEwen Lake is comparable with that of Lake Huron (Van Oosten, 1939) and with Pigeon Lake, Alberta during those years when growth was particularly good there (Miller, 1956). It is slightly greater than that of Lake Erie (Van Oosten and Hile, 1949). Growth in Nueltin and MacDonald is slower than in Lake Erie, but comparable with growth in Lake Winnipeg (Kennedy, 1954). In all three, whitefish grow faster than in Great Slave Lake (Kennedy, 1953) or in Lake Nipigon (Hart, 1931).

MORTALITY RATE

Values at the bottom of Tables I, II and III indicate the numbers of fish of each age in the samples from Nueltin, MacDonald and MacEwen Lakes respectively. "Catch curves", as defined by Ricker (1958), were derived by plotting the logarithm of numbers of fish against age in the three panels of Fig. 2. To derive values for mortality rates, straight lines were fitted by inspection to the right limbs of each catch curve. Appropriate calculations (see Ricker, 1958) based on the slopes of these fitted straight lines yield the following values for

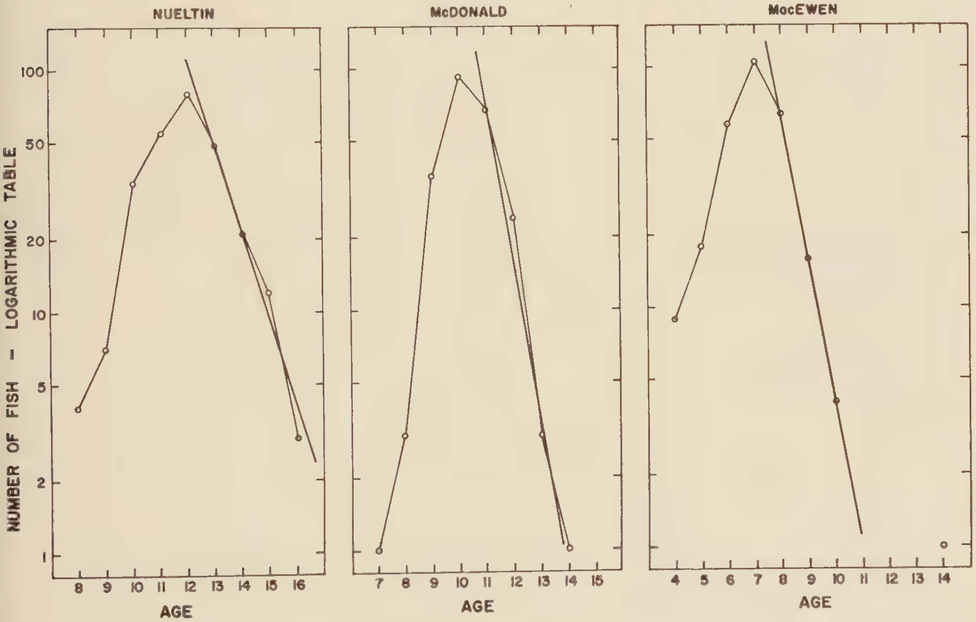

Fig. 2. Catch curves for whitefish from three Northwest Territories lakes. Straight lines are fitted by inspection to the right limb of each catch curve as a basis for computing mortality rates

total annual mortality rates: Nueltin, 57%; MacDonald, 81%; MacEwen, 74%. Taking a specific case as an example, these calculations indicate that 81% of all MacDonald Lake whitefish which are between 11 and 14 years old die each year; that is, out of every 100 fish which become 11 years old, 81 die before becoming 12 years old, and out of the 19 survivors another 81% or 15 die during the following year. So only four live to become 13 years old and less than one lives to become 14 years old out of every 100 that become 11 years old.

These mortality rates are of particular interest because, until the time that the respective samples were taken, exploitation by man had been a negligible cause of death. In other words, the values—Nueltin 57%, MacDonald 81% and MacEwen 74%—represent natural mortality rates as defined by Ricker (1958).

Natural mortality was estimated to be 61% among unexploited whitefish from Great Slave Lake on the basis of a much larger sample (Kennedy, 1953). Ricker (1949) derived smaller values for natural mortality among the unexploited whitefish of Shakespeare Island Lake and of Lake Opeongo.

ACKNOWLEDGMENTS

Assembling the material for this paper has required the cooperation of a number of people. It is a pleasure to have this opportunity to thank those specifically mentioned in the text for their assistance. I am also greatly indebted to Mr J. J. Keleher for extensive help with preparation and tabulation of the data.

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Three Records of the Black Scabbard Fish, *Aphanopus carbo* Lowe, from the Canadian Region of the Western Atlantic[1]

By Wilfred Templeman and H. J. Squires

Fisheries Research Board of Canada
Biological Station, St. John's, Nfld.

ABSTRACT

Two female specimens of the black scabbard fish, 103 and 109 cm long, were captured by otter trawl at 380–400 fathoms (695–732 m) on the Northeast Newfoundland Shelf, on September 30 and October 5, 1959. An additional specimen, a 110–cm female, was caught by longline at over 300 fathoms (> 550 m) off Sable Island Bank in mid August 1960. Meristic, body–proportion and other characteristics of these specimens were within the possible range of variation for *Aphanopus carbo* Lowe from the eastern Atlantic.

INTRODUCTION

On September 30, 1959 a female specimen of the black scabbard fish, *Aphanopus carbo* Lowe, 103 cm greatest total length, was caught by the otter trawl of the *A.T. Cameron* (Mr T. K. Pitt, Scientist-in-charge), on the seaward slope of the Northeast Newfoundland Shelf in 380–400 fathoms (695–732 m), bottom temperature 3.50°C, at Lat. 52°29′15″N and Long. 51°23′30″W. Again on the same cruise to the NE Newfoundland Shelf, on October 5, 1959 a second female specimen of the same species, about 109 cm greatest total length, was caught in 380–390 fathoms (695–713 m), bottom temperature 3.48°C, at Lat. 50°56′30″N and Long. 50°31′52″W.

In mid August 1960 a third female specimen of *Aphanopus carbo*, about 110 cm greatest total length, was caught by Mr Russell Decker of Lockeport, Nova Scotia, on a halibut longline on the seaward slope of the southwestern edge of Sable Island Bank in over 300 fathoms (> 550 m). (Reported as *Aphanopus* sp. ? by Leim and Day, MS, 1961.)

The 2 Newfoundland specimens of *Aphanopus* were preserved in 10% formalin and later examined in detail by the authors. The Sable Island Bank specimen was kept in a frozen condition for about 16 months before being placed in 10% formalin and examined in detail by the senior author.

INFORMATION

Figure 1 shows these 3 specimens of *Aphanopus*, Fig. 2 the heads, and Fig. 3 a ventral view of the anal spines and the neighbouring cloacal region.

To our knowledge these are the first records of this fish west of East Greenland. For this reason, and because until recently (Tucker, 1956) a number of

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[1] Received for publication March 19, 1962.

J. Fish. Res. Bd. Canada, 20(2), 1963.
Printed in Canada.

supposed species of *Aphanopus* have been confused, we have examined these fish in some detail to make certain of their species. In Table I the results of our examinations are compared with data on *Aphanopus* from Tucker's review of the genus.

DISCUSSION AND CONCLUSIONS

Until rather recently there has been considerable confusion regarding definition of species in *Aphanopus*. The original description of *Aphanopus carbo* was by Lowe (1839) of a specimen from Madeira, but Lowe described the fish in generic rather than in specific detail. *Aphanopus minor* was established by Collett (1887) on a specimen with an imperfect tail from Denmark Strait off East Greenland. These imperfect descriptions allowed Saemundsson (1907) to describe an Icelandic specimen as *Aphanopus schmidti*. Subsequently *Aphanopus microphthalmus* was described by Norman (1939) from a Gulf of Aden specimen.

Tucker (1956) examined the holotypes of these nominal species, including Lowe's original specimen, and compared them with about 30 specimens from Madeira and with the same number from the northeast Atlantic. He concluded that these species of *Aphanopus* could not be distinguished and that consequently there was only one species, *Aphanopus carbo* Lowe.

Our 2 specimens of *Aphanobus* from the Newfoundland region have meristic, body-proportion and other characteristics in general agreement with those attributed to the European specimens of *Aphanobus carbo* by Tucker and other authors (Table I), with the exception that the caudal and total vertebrae are 1 beyond Tucker's range.

Specimen No. 2, although only slightly longer, was considerably sturdier and heavier than Specimen No. 1. In Newfoundland Specimen No. 2 (Fig. 2) the anterior cartilaginous chin projection of the lower jaw is short compared with No. 1. Thus the lower jaw projects only 0.9 cm beyond the upper, compared with 1.1 cm for the (smaller) No. 1 specimen.

The Sable Island Bank specimen (Table I, Fig. 1–3) was considerably heavier, for its length, than the Newfoundland specimens. Its greatest body depth is somewhat greater than that ascribed to the *Aphanopus carbo* of the eastern Atlantic by Tucker (1956). Greatest depth, however, is highly variable in many fishes. The orbital length is less than in the 2 Newfoundland specimens but this may have been due partly to drying and shrinking under refrigeration. The dorsal and anal rays could not be counted. The caudal vertebrae were one beyond the range of Tucker's eastern Atlantic specimens, the pre-caudal vertebrae were 2 greater, and the total vertebrae 4 greater. The general characteristics, including the anal spines, pectoral rays, black colour, tail length, snout length, head length, etc., were within the *Aphanopus carbo* range. It is concluded that this specimen, also, is close enough to the *Aphanopus carbo* of the eastern Atlantic to be assigned to this species.

In vertebral number our specimens are slightly above the higher limit of the range for the eastern Atlantic. Consequently it is possible that passing westward in the Atlantic *Aphanopus*, like the cod (Schmidt, 1930), possesses higher vertebral numbers than toward the east.

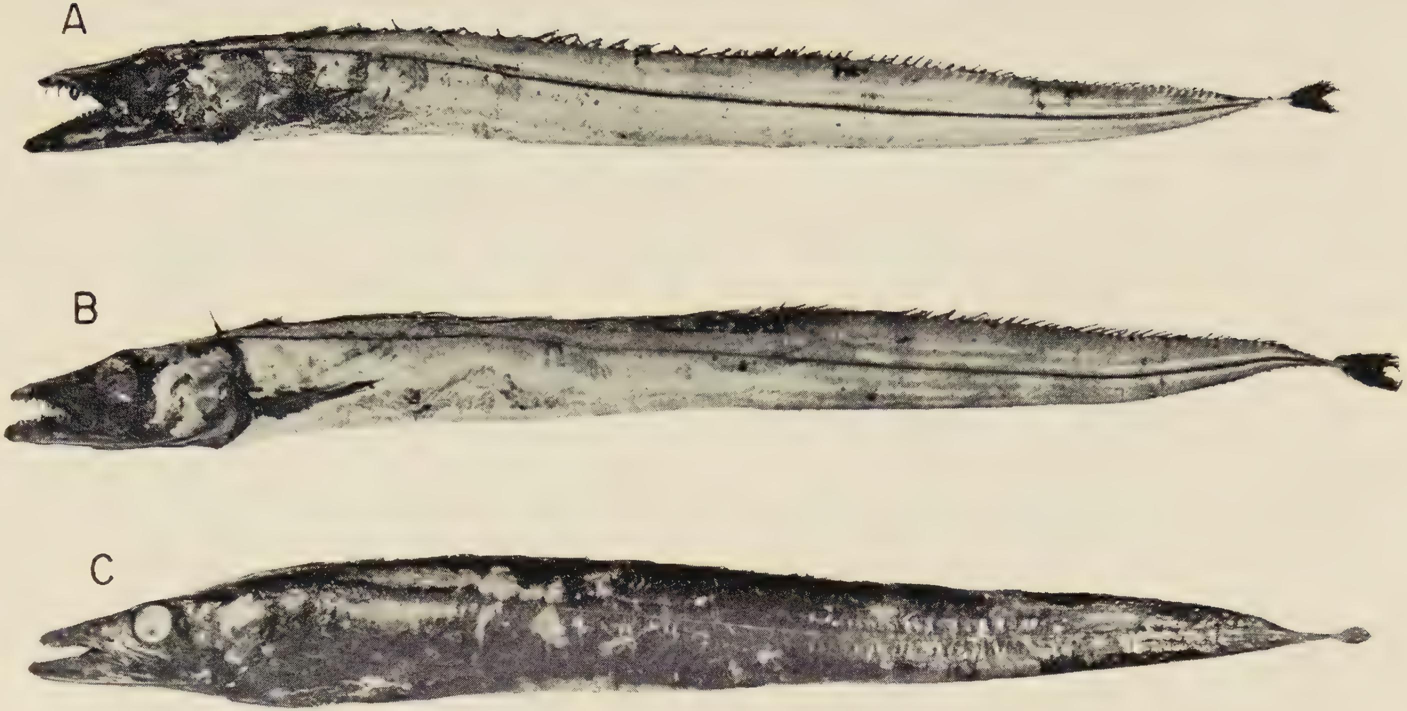

FIG. 1. Three female black scabbard fish, *Aphanopus carbo*, caught in the Canadian region of the western Atlantic: A, Northeast Newfoundland Shelf specimen No. 1 (of Table I) Sept. 30, 1959, 103 cm long; B, Northeast Newfoundland Shelf specimen No. 2, Oct. 5, 1959, *ca*. 109 cm long; C, Sable I. Bank specimen, mid-August 1960, *ca*. 110 cm long. (In A and B the glossy coal-black epidermis has been lost from most of the body, remaining only on parts of the head and on the pectoral and caudal fins and in a few spots on the body.)

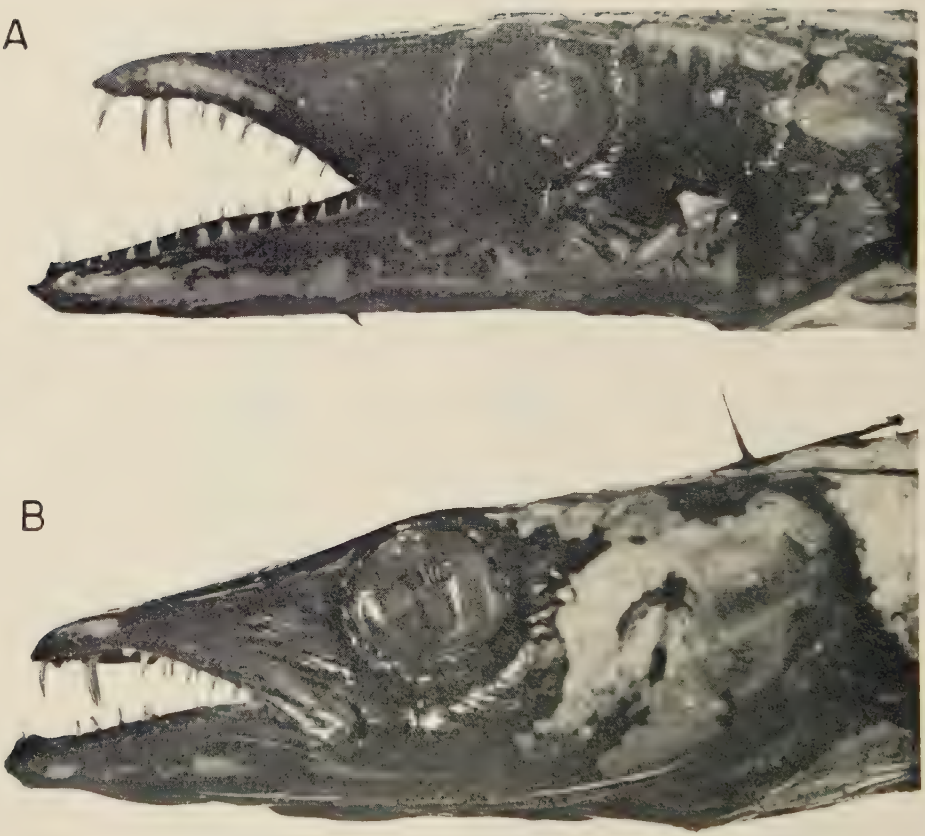

FIG. 2. Enlarged heads of *A. carbo* of Fig. 1: A, Nfld. specimen No. 1; B, Nfld. specimen No. 2.

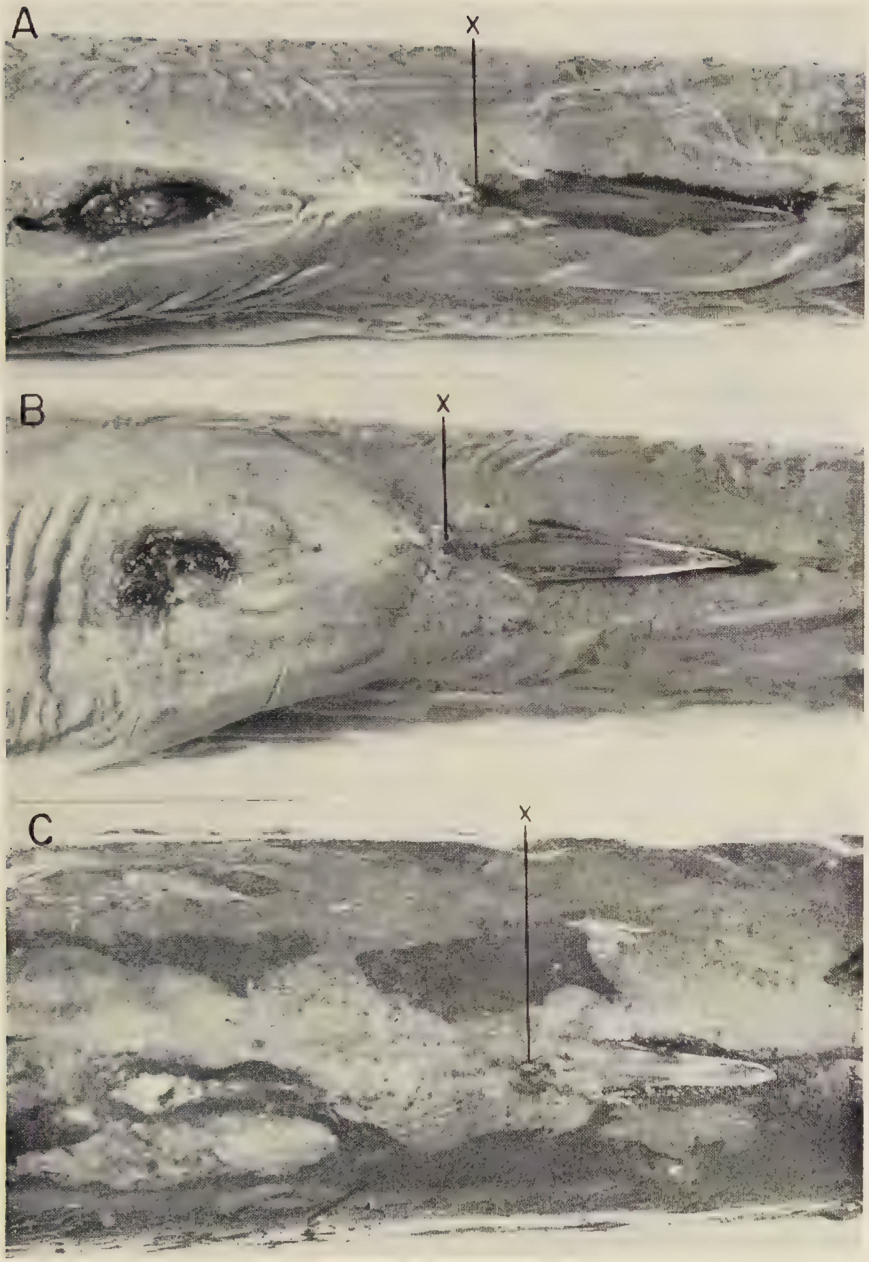

FIG. 3. Ventral views of anal spines and cloaca of *A. carbo* of Fig. 1: A, Nfld. specimen No. 1; B, Nfld. specimen No. 2; C, Sable I. Bank specimen. (× 1.6. Line marked "X" shows position of first small anal spine at base of large anal spine.)

The large anal spine and the position of the rudimentary first anal spine are shown in Fig. 3.

Until fairly recently *Aphanopus carbo* was considered to be a rare fish in the northeast Atlantic. Up to 1939, among others, it had been reported from the following localities: off Madeira (Lowe, 1839); Denmark Strait, East of Greenland 65°N, 31°W (Collett, 1887); Scotland (Sim, 1898; see Tucker, 1956); 120 km NW of the Faroes (Collett, 1905); South Iceland (Saemundsson, 1907); up to 1934 many specimens from the south coast of Iceland and 1 off Andenes, Norway (Saemundsson, 1949); and from the Gulf of Aden (Norman, 1939).

Tucker and Palmer (1949) give 37 British records of *Aphanopus carbo* from 1913–1949 and mention other occurrences indefinite in number. These authors also give references, additional to those quoted in the present paper, to captures of this species off Portugal and Iceland. We have not made an exhaustive search of the literature but in recent years there have been numerous records from the eastern Atlantic: from the western shelf of the British Isles and the neighbouring George Bligh and Rockall Banks (Rae and Wilson, 1951, 1954; Rae and Lamont, 1959a, 1959b, 1960, 1961a); from the Rosengarten between the Faroes and Iceland (Brandes *et al.*, 1953, 1954, 1956, 1957); Iceland (Rae and Wilson, 1952; Brandes *et al.*, 1953); from the Anton Dohrn Bank, East Greenland (Krefft, 1959); and the Spanish Coast (Navaz, 1961). Tucker (1956) has also examined 30 specimens from off Madeira and as many more from the northeast Atlantic.

Aphanopus carbo, usually being pelagic in very deep water, generally escapes capture by bottom otter trawls. However, it cannot be a rare fish in the eastern Atlantic because, apart from the above and doubtless many other records, Tucker (1956) says that it has been found to be common along the 100-fathom (180-m) line west of the British Isles, where it may sometimes be taken even by hundreds, by vessels trawling for hake. Saemundsson (1949) notes that many specimens, as many as 10 on a single trip, have been taken by longline south of Iceland. Maul (1945) says that there is an established longline commercial fishery off Madeira for *Aphanopus carbo*, between 350 and 800 fathoms (640–1460 m). Figueira (1957) also reports a commercial fishery for *Aphanopus carbo* off Madeira by small boats fishing in 600–1000 m.

Although Goode and Bean (1895) make the statement (attributed to Capello) that specimens of 4 or 5 feet (*ca.* 120–150 cm) long have been taken by longline fishermen from Madeira, all but one of the north Atlantic length records that we have been able to find have been of 110 cm or smaller: Collett, 1887 (calculated, if normal, *ca.* 70 cm); Collett, 1905 (87 cm); Saemundsson, 1949 (90–110 cm); Tucker and Palmer, 1949 (♀93.5 and ♀110.5 cm); Rae and Wilson, 1953 (98 cm); Brandes *et al.*, 1956 (♀107.5 cm), 1957 (103.5 and ♀107 cm); Krefft, 1959 (♀108 cm); Rae and Lamont, 1961b (103 and 104 cm); Newfoundland specimens, Table I (♀103 cm, ♀*ca.* 109 cm); Nova Scotia specimen (♀*ca.* 110 cm). Navaz (1961), however, describes a 129-cm specimen from a depth of 400 m off San Sebastian, Spain.

TABLE I. Comparison of 3 specimens of *Aphanopus* from the Canadian region with specimens of *Aphanopus carbo* described by Tucker (1956), taken from east Greenland to the Gulf of Aden (the "east Atlantic"). All measurements of the Newfoundland and Sable Island Bank specimens except No. 2 were made after preservation of the fish in 10% formalin, followed by soaking for a day or two in fresh water before measurement. Unless noted otherwise, measurements are horizontal between vertical planes. Values in parentheses are calculated. Footnotes on opposite page.

Character	East Atlantic	Nfld. specimen No. 1	Nfld. specimen No. 2	Sable I. Bank specimen
1. Weight (out of formalin), *kg*	...	1.3	1.8	2.2
2. Greatest total length[m] (fresh), *cm*	...	103	(109)	(110)
3. Greatest total length[m] (formalin), *cm*	...	101	107	...
4. Length to mid-fork of caudal[m], *cm*	...	99	104	(105)
5. Standard length[i] (S.L.), *cm*	...	95.7	100.2	101.9
6. Head length[l] divided	5.7 – 4.9[k]	5.0[a]	5.0[a]	5.1[a]
into S.L.	...	5.2[b]	5.3[b]	5.3[b]
7. Greatest body depth in S.L.	21.7 – 11.2[k]	12.3[c]	11.4[c]	9.1[h]
8. Greatest body thickness in S.L.	...	25.9[c]	25.1[c]	20.4[h]
9. Tail length as	...	44.6[d]	44.7[d]	43.9[d]
percentage of S.L.	48 – 49	49.0[e]	50.6[e]	...
10. Spinous/soft dorsal bases	Sub-equal	0.942	0.995	...
11. Difference between spinous and soft ray bases, as % of S.L.	At most ± 3	2.4	0.2	...
12. Length of anal	...	I. 2.6	I. 2.4	I. 2.0
spines[j], *cm*	...	i. 0.18	i. 0.15	i. 0.10
13. Interorbital — least fleshy width, *cm*	...	3.7	3.8	...
14. Interorbital — least bony width, *cm*	...	2.8	3.0	3.1
15. Greatest length of orbit, *cm*	...	3.9	4.2	3.6
16. Long. diam. eye, cornea only, *cm*	...	3.4	3.6	3.4
17. Diameter of eyeball, *cm*	...	*ca.* 4.1	...	...
18. Snout to anterior wall	...	8.3[a]	8.2[a]	8.0[a]
of orbit, *cm*	...	7.6[b]	7.8[b]	7.8[b]
19. Dorsal spines	38 – 41	38	39	...
20. Dorsal soft rays	53 – 56	56	55	...
21. Total dorsal spines & rays	91 – 95	94	94	...
22. Anal spines[j]	i + I	i + I	i + I	i + I
23. Anal fin rays	44 – 48	47	47	...
24. Pectoral rays	12[f]	13	12	12
25. Vertebrae, pre-caudal	42 – 44	43	43	46
26. Vertebrae, caudal[g]	55 – 56	57	57	57
27. Vertebrae, total[g]	98 – 99	100	100	103
28. Pyloric caeca	...	6	...	...
29. Teeth (including fangs), right half of upper jaw	...	10	12	...
30. Teeth, right half of lower jaw	...	14	12	...
31. Total fangs (on upper jaw)	...	4	4	...
32. Principal teeth of maxillary and dentary series without barbs	Yes	Yes	Yes	...
33. Ventrals, external	None	None	None	...
34. Stomach	...	Everted	Everted	...
35. Colour	Uniform black when dead	Black	Black	Uniform black
36. Sex and maturity	...	♀	♀ spent, maturing	♀ maturing
37. Diameter of eggs, *mm*	...	0.2	0.2	0.4

ACKNOWLEDGMENTS

The authors are very grateful to Mr T. K. Pitt who collected the Newfoundland Shelf specimens, to Dr J. L. Hart and Mr L. R. Day for the privilege of examining the Nova Scotia specimen and including it in this paper, to Dr D. W. Tucker who provided several references, and to Mr E. L. Rowe who did the photography.

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[a] Measured directly, along the surface of the body.

[b] Measured horizontally, between vertical planes.

[c] Greatest depth and greatest thickness were at the posterior tip of the pectoral fin.

[d] Middle of cloaca to posterior end of hypurals.

[e] Middle of cloaca to tip of caudal fin when extended directly backward.

[f] From Saemundsson (1932).

[g] Including the urostylar half-vertebra as 1 vertebra. The first caudal vertebra was that bearing a closed haemal arch with a haemal spine and was (as in Tucker 1953, pl. 2, fig. 2) the first vertebra completely behind the combined interhaemals forming the internal base of the large anal spine. Tucker (personal communication, Feb. 24, 1962) says that in his work on *Aphanopus* the urostylar half-vertebra was counted as a vertebra.

[h] Opposite the mid-pectoral.

[i] Length from the snout to the end of the hypural plate.

[j] I = large anal spine; i = small anal spine at anterior base of large anal spine (Fig. 3).

[k] Range corresponding to S.L. range from 10 to 104 cm.

[l] Snout to the posterior edge of the opercular membrane.

[m] These lengths were measured from the anterior tip of the chin. The tips of the caudal fins of the Newfoundland specimens were not perfect and several millimetres at least are missing from the greatest total length, at least from the length measured after being in formalin. In the Sable Island Bank specimen even more of the caudal fin was broken off, and the length to the mid-fork was corrected by comparing it with Newfoundland specimen No. 2.

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Summer Food of Lake Whitefish, *Coregonus clupeaformis* Mitchill, from Heming Lake, Manitoba[1]

By N. H. F. Watson[2]

Fisheries Research Board of Canada
Biological Station, London, Ont.

ABSTRACT

During the summer months of 1956 to 1959 inclusive, the stomach contents of 2963 Heming Lake whitefish from 5–15 inches in length were examined. Data on stomach contents of 194 whitefish taken in 1945 were examined and included in this analysis. Most stomachs contained food, but lesser quantities of food per stomach and many empty stomachs were found in July and August of each year. Mayfly nymphs occurred in the stomachs most often. Other insects eaten included dipterous larvae, especially *Chaoborus* and chironomids. Incidental items, constituting a smaller though important part of the fish's diet, included aquatic coleopterans, hemipterans, trichopteran larvae, cladocerans, *Hyalella*, hydrachnids, gastropods and, seasonally, aerial insects from the surface of the lake, and small fish. Cyclopid and calanoid copepods were found in about 1% of the stomachs. This apparently low incidence of cyclopids in the diet is considered to be sufficient to establish the relatively high infection levels of *Triaenophorus* found in Heming Lake fish. Some differences in diet between fish of different sizes and between seasons were shown.

INTRODUCTION

This paper reports on the stomach contents of samples of lake whitefish, *Coregonus clupeaformis* Mitchill, taken during experimental gill-net operations at Heming Lake, Manitoba in the summer months of the years 1945 and 1956 to 1959. The data were collected as part of an ecological study of the pike–whitefish tapeworm, *Triaenophorus crassus* Forel, by personnel of the Fisheries Research Board of Canada.

The limnology of Heming Lake has been described by Lawler and Watson (1958). It is a small, shallow, unstratified lake in the glaciated Precambrian Shield in northern Manitoba. Lake temperatures are strongly influenced by existing air temperatures and oxygen content approaches saturation with constant mixing. Fifteen species of fish occur in the lake, including the northern pike, *Esox lucius* Linnaeus; lake whitefish, *C. clupeaformis;* and the cisco, *Leucichthys* sp. These three species are involved in the life cycle of *Triaenophorus crassus.* The pike is the final host, and the two coregonines are second intermediate hosts.

The stomach contents of whitefish were examined during the summer to see if any marked changes in diet of the fish occurred during the different time periods, and to learn if the food habits of whitefish of different sizes might be related to *Triaenophorus* infection.

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[1] Received for publication September 18, 1962.

[2] Present address: Laboratory of Parasitology, Dept. of Biology, Wayne State University, Detroit 2, Michigan.

J. Fish. Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

MATERIALS AND METHODS

In 1945 Dr W. M. Sprules examined the stomachs of 194 whitefish. The fish in these samples ranged between 11 and 17 inches (28–43 cm) in length and averaged 14.6 inches (37.1 cm) long. Since the lengths and stomach contents of individual fish were not available, only a summary analysis of the stomach contents is presented here for comparative purposes.

During the summer months, May to September, 1956 to 1959, stomachs from 2963 whitefish from Heming Lake were examined. The fish were mostly small, averaging 8.6 inches (22 cm) in length. They were captured in one-night sets of nylon gill nets with mesh size ranging from 1½–5 inches (3.8–12.7 cm), stretched measure. Stomach contents of about three-quarters of the total catch for each of the four summers were examined fresh, and items present were recorded along with the length data.

In examination, the complete stomach was removed, slit lengthwise, and the contents were turned on to a flat dish, teased out under water and examined. Small food items in the mucous lining of the stomachs were identified with a stereoscopic dissecting microscope. The food items present in each stomach were recorded and the number of stomachs containing each food item was determined.

Individual food items were counted for some categories, but for the most part it was impossible to enumerate exactly the number of partly digested, soft-bodied invertebrates found in the stomachs. Thus the chief measure of the food of the whitefish in this study is the number of stomachs containing each item. This, coupled with the number of empty stomachs and visual estimates of the relative volume of each item eaten, was used to determine the importance of any item in the diet of the fish.

The number of fish with stomachs containing each food item and the number with empty stomachs was recorded for each monthly period by length intervals of 1 inch (2.5 cm). In an attempt to keep the groups large enough for adequate analysis, all the fish less than 5.5 inches (14.0 cm) were included in the 6-inch (15.3-cm) category and those over 13.6 inches (34.5 cm) were put in the 13-inch (33.1-cm) and over group. Table I shows the number of stomachs examined

TABLE I. Number of whitefish examined for stomach contents by monthly periods, 1956–1959.

	1956	1957	1958	1959
May	...	82	164	11[a]
June	...	199	358	69
July	71	249	618	228
August	203	216	304	27
September	52	59	64	4[a]
Total:	326	805	1508	339

[a] These samples are not included in subsequent stomach analyses.

each month of the four years when samples were taken, and Table II shows the length frequency of the fish examined. It was impossible to compare yearly differences in diet for all years, since adequate samples were taken in all five summer months only in 1957 and 1958. Because the differences in the proportion of items eaten in these two years appeared slight, it was decided to combine the samples for each month from all years to compare seasonal changes in the diet.

The number of fish with empty stomachs and with each food item was adjusted to a standard base of 100 fish examined per length group for each month.

TABLE II. Length frequency of whitefish examined for stomach contents, 1956–1959.

Length						
Inches	Centimeters	1956	1957	1958	1959	Total
4.6–5.5	11.7–14.0	28	42	...	2	72
5.6–6.5	14.1–16.5	33	297	170	39	639
6.6–7.5	16.6–19.0	31	72	265	12	380
7.6–8.5	19.1–21.6	8	62	461	57	588
8.6–9.5	21.7–24.1	30	42	316	64	452
9.6–10.5	24.2–26.7	62	38	146	30	276
10.6–11.5	26.8–29.2	53	49	85	65	252
11.6–12.5	29.3–31.8	29	66	40	36	171
12.6–13.5	31.9–34.3	19	67	16	14	116
13.6–14.5	34.4–36.9	9	45	5	3	62
14.6 and over	over 37.0	24	25	4	2	55

RESULTS

Most of the common species of benthic invertebrates from Heming Lake' listed in a previous paper (Lawler and Watson, 1958), were found in the whitefish stomachs examined from 1956 to 1959. Aerial insects, fish remains and planktonic organisms were eaten as well. Some stomachs contained plant material such as staminate pine cones from the surface and leaves of *Potamogeton*.

The food items from the stomachs were placed in one of 15 categories for the purposes of analysis. Those items which were found in more than 5% of the stomachs from any one month (on an adjusted basis) are shown graphically in the figures. The remainder included a few miscellaneous insect forms such as *Sialis* and caddis larvae, plant remains, bottom ooze with associated small invertebrates such as ostracods, and copepods.

Most mayfly nymphs found were *Hexagenia* spp., although some *Ephemerella* spp. and *Tricorythodes* spp. were noted. Mayfly nymphs and *Chaoborus* were volumetrically the most important food items. The most abundant cladoceran in the stomachs was *Daphnia* sp., but *Holopedium gibberum*, *Leptodora kindtii* and *Diaphanosoma brachyurum* were present also. The gastropods were mainly *Amnicola* spp. No attempt was made to identify the several species of notonectids, coleopterans, hydrachnids or chironomids found in many stomachs. Miscellaneous dipterous larvae found in a few stomachs included ceratopogonids, tabanids and culicids. Most of the aerial insects eaten by the whitefish were mayfly adults although ants, wasps and mosquitoes were present in some stomachs, apparently taken from the surface of the lake. Several species of small fish including yellow perch, *Perca flavescens*; white sucker, *Catostomus commersoni*; pike fry; ninespine sticklebacks, *Pungitius pungitius*; and a Johnny darter, *Etheostoma nigrum*, were found in stomachs. Unidentified fish eggs were eaten by a few fish in May.

The copepods eaten included the calanoids, *Diaptomus* spp. and *Ephischura* spp., and the cyclopids *Eucyclops agilis*, *Mesocyclops edax*, *Cyclops bicuspidatus thomasi* and *Cyclops brevispinosus*. Of these, only the last two are considered to be naturally occurring first intermediate hosts of *Triaenophorus crassus* in the lake (Watson and Price, 1960). About 2% of the stomachs contained either calanoid or cyclopid copepods. About half of these contained cyclopids which are known to act as vectors for *T. crassus*. Very few of these were found in any one stomach, in contrast to cladocerans which were found in large quantities in many stomachs.

Most of the above items were found in the stomachs of the fish examined in 1945 (Table III). In addition, leeches and crayfish remains were found in some of those examined in May and June of that year.

TABLE III. Percentage analysis of the stomach contents of the 194 whitefish taken from Heming Lake from March 2 to September 6, 1945. (Data collected by Dr W. M. Sprules.)

	Percentage frequency			Percentage composition			Percentage volume		
Food Item	Mar. 2 to Mar. 6	May 23 to June 23	Aug. 28 to Sept. 6	Mar. 2 to Mar. 6	May 23 to June 23	Aug. 28 to Sept. 6	Mar. 2 to Mar. 6	May 23 to June 23	Aug. 28 to Sept. 6
Hirudinea	...	6.5	...	...	0.2	...	...	1.0	...
Crustacea	...	60.9	8.0	...	11.7	0.6	...	3.5	T
Arachnida	5.3	28.3	2.0	1.0	14.9	0.3	T	6.3	T
Insecta	100.0	97.8	98.0	70.9	54.6	52.2	96.1	76.4	90.0
Mollusca	71.1	43.5	30.0	28.1	17.0	46.9	3.9	8.8	10.0
Pisces	...	6.5	...	...	0.3	...	...	3.9	...
Eggs (fish)	...	8.7	...	...	1.4	...	...	?	...
Plant remains	1.3	30.4	4.0	...	...	...	T	?	T

Monthly changes in the prevalence of the various food items were compared by summing the adjusted frequency of occurrence for each item in all the length categories for that month. A graphical analysis of the changes in the abundance of the more frequently occurring food items found in stomachs and of empty stomachs is given in Fig. 1. Some evidence of the seasonal nature of certain items in the diet may be seen from the graphs.

Empty stomachs were few in May and June, their number increased through July and rose to a peak in August and declined somewhat in September. This was coupled with a decline in the volume of food in the stomachs in July and August noted in estimates made of stomach contents. Many fish in these months had only traces of food in their stomachs. Also, as seen from the graphs, many

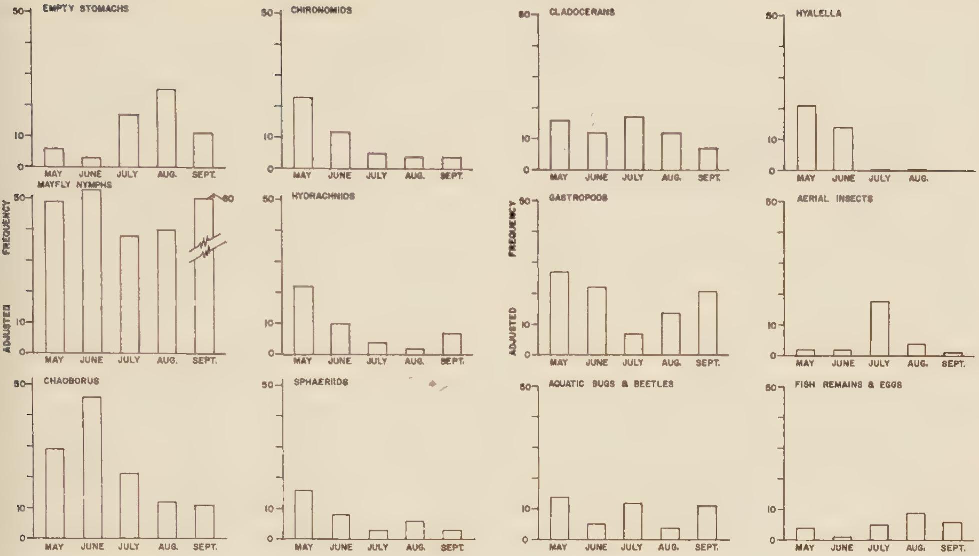

FIG. 1. Monthly variation in adjusted frequency of empty whitefish stomachs and those food items occurring in more than 5% of the stomachs (based on equal numbers of fish from each length group adjusted to a base of 100 fish for each month).

food items declined in frequency in the diet from a peak in May and June to a low in September. Such items included *Chaoborus*, chironomids, *Hyalella azteca* and hydrachnids. The frequency of stomachs containing mayfly nymphs and gastropods declined in July and August, but increased in September.

The frequency of several items, cladocerans, aquatic bugs, beetles, and sphaeriids remained low and relatively constant throughout the season, tending to decline slightly in August and September. Emergent mayflies and fish remains were encountered in numbers and largest volume only in July or August.

Since the frequency of some items at least appears to be related to the time of year, the analysis of diet with length must also take this factor into consideration. Therefore, plots were made of the adjusted incidence of each of the major items of the diet against length of fish for each of the summer months. From Fig. 2, trends for selected items with size for each month can be determined.

Stomachs of the smallest fish most frequently contained *Chaoborus*, chironomids, other dipterous larvae, cladocerans and hydrachnids. These items declined in frequency in the stomachs examined as the size of fish increased. The frequency of stomachs containing mayfly nymphs, other large aquatic insects and gastropods increased as the size of the fish increased. Some of the stomachs of the larger fish, however, contained considerable quantities of *Chaoborus* and cladocerans. *Hyalella azteca* was apparently ingested more frequently by fish in about the middle of the size range than by larger or smaller fish in the two months when it was eaten.

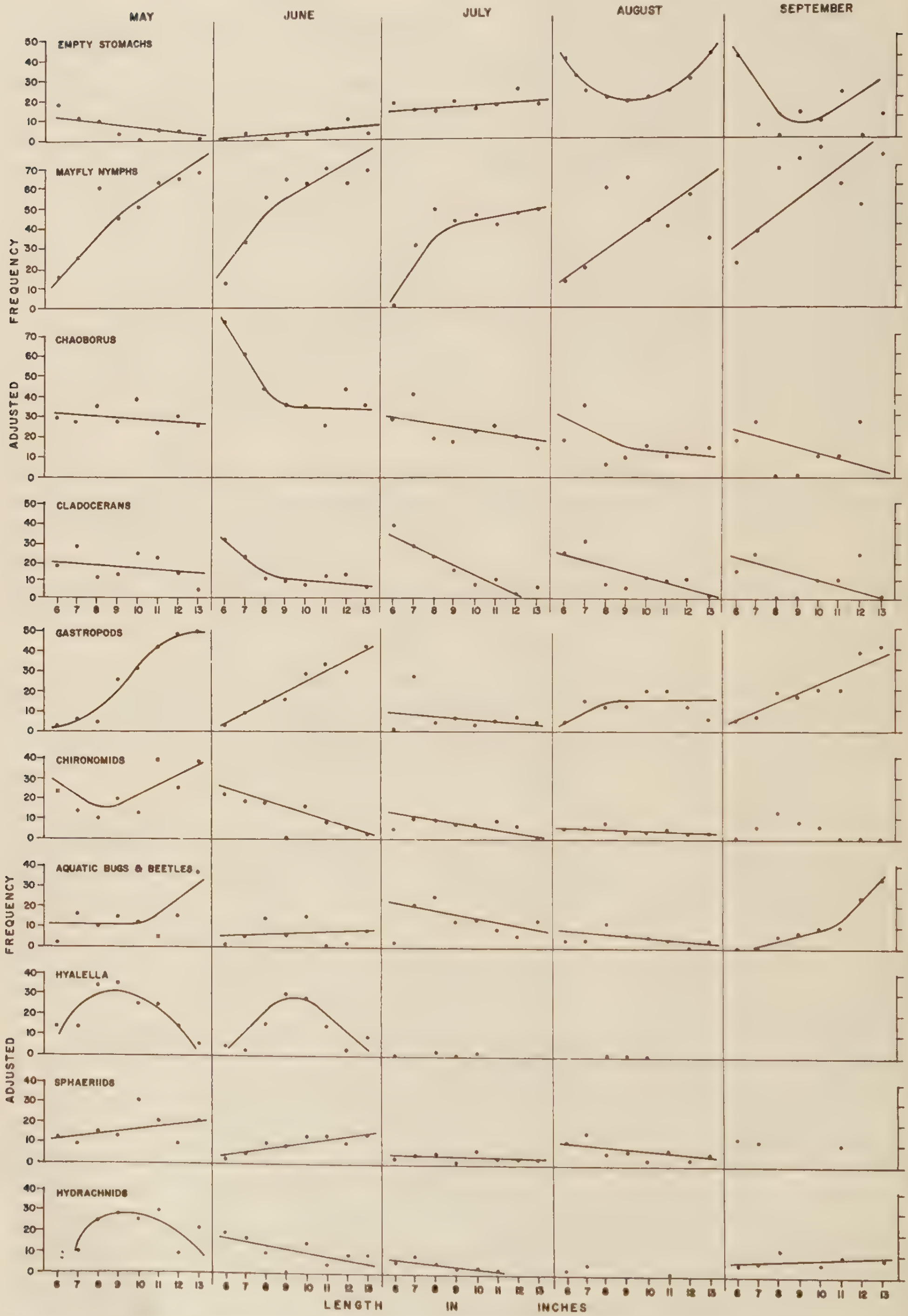

FIG. 2. Adjusted frequency of major food items in stomachs of whitefish of various lengths based on a sample of 100 fish of each length group each month.

DISCUSSION

The major item in the diet of the whitefish from Heming Lake was found to be mayfly nymphs. Dredgings in the lake indicate that these are the most numerous of bottom organisms. From this it can be deduced that availability of food is more important than any selection by the fish. This also is demonstrated by the seasonal importance of the emerging and adult mayflies present at the surface of the lake in July. Other authors, Hart (1931) and Quadri (1961), have concluded that availability is the chief factor influencing the composition of the diet of whitefish.

At least two factors may be of importance in determining this availability. These are time of year and size of fish. The diet was most varied and largest quantities of food were eaten per fish during the months of May and June. This coincides with the period before the summer emergence of the Diptera and mayflies from the lake. Some items such as *Hyalella*, which were present in dredgings through the summer, were eaten in quantities only seasonally. It is therefore necessary to contrast availability to the fish with mere presence of the item in the lake. Smaller fish had a different diet than larger fish, and some items replaced others as size increased.

Since it is believed that whitefish obtain plerocercoids of *Triaenophorus crassus* by eating infected *Cyclops*, the low frequency of cyclopid copepods in the diet of the whitefish is noteworthy. No more than 1% of all stomachs examined were found with cyclopids and none of these stomachs contained more than a few individuals. The copepods were found in all months in fish from 5 to 12 inches (12.7 to 30.5 cm) in length.

The incidence of cyclopids infected with procercoids of *Triaenophorus* from selected areas of the lake in the spring of the four years was about 1% when all samples are combined, but samples with as much as one-third infection were found, suggesting that there may be local concentrations of infected plankters (Lawler and Watson, unpublished data).

In the absence of any data on the food of whitefish less than 5 inches (12.7 cm) and more precise information on the distribution of the infected cyclopids, there is very little more that can be said about the relationship between the food of the whitefish and *Triaenophorus* infection. It would seem unlikely on the basis of chance encounters alone that infections would take place more than rarely. The effect of aggregations of infected *Cyclops* suggested above would certainly improve the chance of infection. There are no apparent differences in food from the 1945 samples examined by Sprules. The small number of *Cyclops* eaten seems sufficient to establish infection with *Triaenophorus*.

Fraser (1960) investigated an outbreak of diphyllobothriasis in trout in a reservoir in west England and found a similar low incidence of infected first intermediate hosts in the plankton sufficient to increase the level of infection in the trout in successive year-classes after the first. In both these fish and the Heming Lake whitefish, the apparent number of fish found eating copepods and the quantities of copepods eaten were very low.

The low frequency of copepods in whitefish stomachs of all sizes examined, coupled with the low percentage of infected copepods, illustrates the extreme difficulty which would be experienced in attempting to eliminate the parasite by controlling the first or second intermediate hosts by methods practical at present.

ACKNOWLEDGMENTS

Mr G. P. McRae assisted in the collection of the whitefish stomachs. Dr G. H. Lawler and Mr J. J. Keleher, Fisheries Research Board of Canada, and Dr D. L. De Giusti, Wayne State University, reviewed the manuscript at several stages and offered valuable comments and criticism.

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Some Aspects of Olfactory and Visual Responses in Pacific Salmon[1,2,3]

By J. R. Brett and C. Groot

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Past and current research by the Fisheries Research Board of Canada related to olfactory and visual responses in Pacific salmon is reviewed, including comments on some of the sensory and behavioural relations important in migration.

An innate ability to perceive highly dilute odours supports the view that olfaction can be instrumental in detecting a distant source, but the problems of following a well directed course indicate likely support from other sensory paths including visual and acoustico–lateralis responses.

A threshold visual sensitivity of about 1/300 that of bright moonlight and an ability to orient at night, with view of the sky only, provide evidence that retinal images may be useful as migratory cues as long as turbidity does not interfere.

INTRODUCTION

Although the opportunity for making comprehensive studies on sensory perception in Pacific salmon (genus *Oncorhynchus*) has not been afforded, a number of observations of rather divers nature have accumulated. The stimulus for these studies has come mainly from two sources. The acute problem of safeguarding migrating salmon from destruction at hydro-electric dams has resulted in intensive efforts to guide salmon, supported by some relevant studies on sensory perception. The fascinating question of how salmon can make precise homing migrations over distances frequently exceeding 1000 miles has been the other stimulus. Olfactory and visual perception have received most attention with some examination of auditory responses reported by Moore and Newman (1956), but no pertinent observations on such sensory systems as gustatory, lateralis, labarynth, and proprioceptor yet published. Fairly detailed descriptions of some aspects of freshwater migration and behaviour are accumulating (Hoar, 1954, 1958; Neave, 1955; Ellis, 1961) providing a basis for speculation on the mechanics of migration. However, until a sound basis for the sensory mechanism can be established, migration will likely remain in the descriptive stage, a phenomenon without diagnosis.

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[1] Received for publication June 25, 1962.

[2] Paper No. 8 concerning the physiology and behaviour of salmonid fishes, from the Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C.

[3] Presented at the TENTH PACIFIC SCIENCE CONGRESS of the Pacific Science Association, held at the University of Hawaii, Honolulu, Hawaii, U.S.A., 21 August to 6 September, 1961, and sponsored by the United States National Academy of Sciences, the Bernice Pauahi Bishop Museum, and the University of Hawaii.

J. Fish. Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

ODOUR RESPONSES

REPELLENT IN MAMMALIAN SKIN

Adult coho (*O. kisutch*) and spring salmon (*O. tshawytscha*) show a marked alarm reaction to water rinses of mammalian skin when experienced at the stage of upstream migration fresh from the sea (Brett and McKinnon, 1954). Efforts to extract the active component and to determine threshold levels revealed that a simple polypeptide was involved, probably containing the amino acid l-serine in its linkage, and detectable at a dilution of at least 1 part in 8×10^{10} water (Alderdice *et al.*, 1954; Idler *et al.*, 1956, 1961). The sensitivity at such great dilution to an organic substance indicated probable detection by olfaction. Under constant application normal migratory behaviour returned within 40 minutes. Olfactory fatigue or supression was likely involved, although the migratory drive may have been sufficient to redominate the behaviour.

Since these original findings other general observations and some specific programs have been conducted. All five North American species of mature *Oncorhynchus* show similar reactions. The young downstream migrants, however, are insensitive or at least unresponsive. Spawning adults exhibit a greatly reduced alarm in which territorial defense and aggressive display appear to suppress retreat. Large doses of odiferous materials such as the sulphurous mixtures in pulp-mill effluent did not affect migration rate nor the subsequent detection of dilute skin rinses while ascending a fish ladder.

The ability for distant or downstream detection of potential predators, among which black, brown and grizzly bear are common members, as well as seals and sea lions, has obvious value. Since the reaction is exhibited by all test fish it is unlikely that learning is the main process. Consequently it can be categorized as an ontogenetically timed, innate, olfactory response producing alarm reactions of significance in survival.

ODOUR ATTRACTANTS

The large size of the olfactory tracts and lobes in the brain of salmon brings emphasis to the potential importance of this sense organ in many aspects of living. Cultured young sockeye show an ability to detect aqueous extracts of brine shrimp at a dilution of 1 part wet weight[4] in 8×10^5 parts water (McBride *et al.*, 1961) provided the shrimp have previously been included in the normal diet. Otherwise no response is observable. Apparently some of the early feeding reactions are to snap at almost any small particle, thereby learning the desirable from the undesirable. Gustatory as well as visual and olfactory senses are involved. In this rapid learning process, and again because of the dilution, it is apparent that olfactory detection can play a significant role.

White (1934) following observations of the entry of adult Atlantic salmon in a previously barren stream where young had been planted the previous year suggested the possibility of attraction from the premature ripening of some of the temporarily resident young salmon. In an effort to test this among Pacific salmon, mixtures including uncontaminated excretory products, ripe ova and testes of coho salmon were released into a fish ladder where upstream migration was in full progress (Brett and MacKinnon, 1954). These excretory and reproductive products did not intensify or appreciably alter the behaviour. It is well known that fish can be conditioned to detect the presence of other species by olfaction (Wrede, 1932; Göz, 1941; Keenleyside, 1955). It remains to be proven whether there is any form of natural species odour recognition in Pacific salmon, although some preliminary observations in our laboratory indicate that individual young sockeye react to the apparent presence of others when water from a hidden aquarium containing similar young salmon is introduced.

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[4] Without knowledge of the active component(s) the gross relation has been used. If the fraction of $\frac{1}{100}$ used by Steven (1959) is applied the relation is of the order of 1 part in 10^8 parts water.

HOMESTREAM ODOURS

Hasler (1954, 1957) in conjunction with Wisby (Wisby and Hasler, 1954) has drawn attention to the possibility of odours being effective in the recognition and orientation to a parent stream by the mature adult, naturally conditioned during early life to its particular stream of origin. Earlier experiments by Craigie (1926) who severed olfactory tracts in returning sea-run salmon were quite ineffective in establishing any basis either for or against such an hypothesis. Wisby and Hasler (1954) demonstrated that trained young coho salmon could successfully discriminate between the odours of two Wisconsin streams. Subsequently, selection of a homestream was tested by experimental plugging of the nasal sacs of half the mature coho captured and returned downstream below a fork in the river of choice.

Unfortunately, none of these efforts conclusively proves anything about odours and distant homing, or even near homing, although the suggestion is apparent. "Non-migratory" blunt-nose minnows, if trained, make equally effective selections between the same Wisconsin streams. The adult coho had recently experienced (i.e. smelled, seen, tasted, learned) the river when trapped, tagged, subjected to olfactory occlusion and returned downstream. It was necessary to assume that all the fish had made a correct *first* choice, that it was indeed their homestream, and that the "straying" of nearly one-third of the returning controls (only half recaptured) was not a discrediting factor. Added to the authors' own comments that comparison and elimination of other sensory systems is desirable, all this points up the difficulties inherent in such field programs. It is not without appreciation of the problems involved that certain limitations are singled out. It is, however, imperative to examine all such cases critically since only the fish "knows" what it is selecting.

Although not always sustained, the success of certain geographically distant transplants (Wickett, 1958; Ricker, 1959) in some species does point up the fact that the inherent tendency is not to return to the area of the parent's early history but rather to that of the displaced developing egg or recently hatched young. The homing ability appears to stem from an imprinting of any suitable nursery area rather than the product of evolution of discrete stocks genetically confined to specific geographic areas.

A recent contribution to what might better be called water-quality-detection in untrained salmon has been reported by Idler *et al.* (1961). Excitement behaviour in a large tank containing Cultus Lake adult salmon could be elicited by water from two of its spawning streams whereas a non-productive stream entering the same lake showed negative response. The reaction could be produced by a heat-labile, volatile component fractionated from the "active" water.

ODOUR DISSEMINATION

Any theory of homing based on odours must be in keeping with knowledge of the pattern of odour dispersal and dilution as well as the physiology of sensory perception including such aspects as thresholds, fatigue, interference, and gradients.

Odours can only be defined in terms of receptors. Dyes, water masses of distinctive density, and chemical constituents are the nearest physical or chemical equivalents. These are the common "tools" of oceanographers and of engineers involved with model studies. Continuous introduction of dye into turbulent water can be seen to produce spurs, discontinuities and cells of differing concentrations. If vigorous mixing continues for some time as the labelled water mass moves, general homogeneity results. The masses of turbid water discharging from a major salmon-producing river like the Fraser illustrate the phenomenon in large scale (Fig. 1). Tully and Dodimead (1957) describe these as "discrete, cloud-like masses" . . . . . pointing out "that there is considerable irregularity in

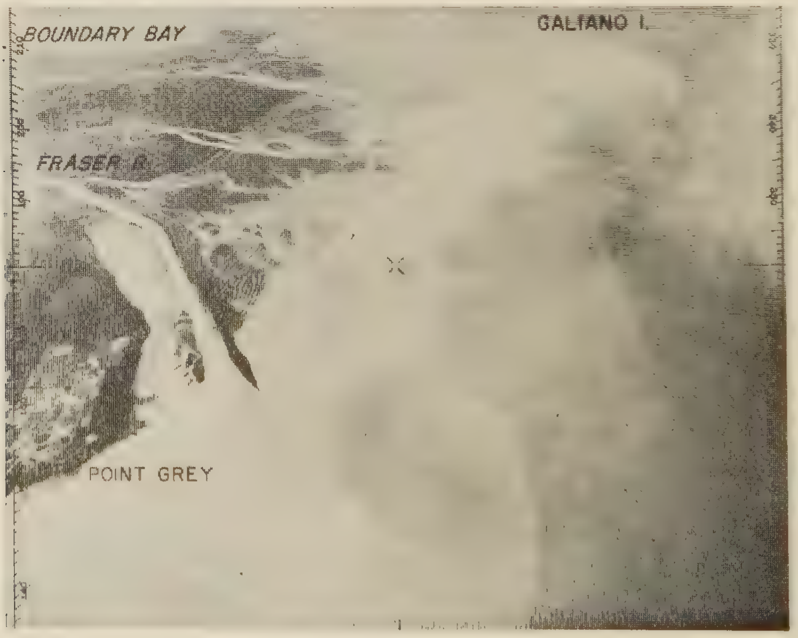

FIG. 1. Aerial photograph of the Strait of Georgia showing Fraser River delta with clouds of silted freshwater along the estuary 2 hours before low tide (from Tully and Dodimead, 1957).

the lateral distribution of salinity". Similarly the outflow of a small stream into a large one where density differences occur from temperature, siltation or dissolved solids carrying entrained odours must result in the same discontinuities. With the exception of very near or final localization of an odour source it is difficult to see how odours could be *directive* at any distance either because of homogeneity or, prior to this uniform dilution, the presence of irregularities which mean that gradients are localized to the "cloud", being greatest at the boundaries and, therefore, not directive to the source. The problem of odour clouds is similarly treated for flying insects by Wright (1958).

The high sensitivity of the olfactory organ indicates the great dilution which is possible before dropping below the threshold of detection. It is sufficient to suggest that if a distinctive odour were present at threshold level, the mixing would likely be sufficient to approach homogeneity. This poses both the question of olfactory fatigue from the continuous presence of a uniform stimulus and alternatively the problem of non-gradient or discontinuous distribution eliminating the possibility of a directive agent. The mammalian repellent, as reported, showed fatigue or suppression in 40 minutes. The necessary slope in gradient of odour to be an effective directing factor would be of interest to know for salmon.

Suffice it to say that with such questions unanswered, distant-homing from a large river estuary remains most enigmatic.

VISUAL RESPONSES

GUIDING EXPERIMENTS

A method of guiding young salmon using a curtain of chains (or cables) spaced 4 to 6 inches apart hung across the path of downstream migration has been shown to be highly effective for deflecting yearling sockeye, and fairly effective for yearling coho (Brett and Alderdice, 1958). Two principles governed the development of the technique—one based on the well known pseudo-rheotropism originally propounded by Lyon (1904) in which stream orientation is maintained by visual cues, and the other on a characteristic of schooling sockeye which show a reluctance to converge in a vertical plane but not so in a horizontal plane (Brett, 1948). Both these phenomena appear to be based on visual responses, in the presence of adequate light.

To substantiate the sensory system involved in chain deflection, a substitution experiment was conducted. By placing glass tubes in the exact position of the chains, deflection was tested with and without the presence of chain inserted *inside* the tubing. By testing throughout the period of nightfall (8–12 PM) the effect of visual versus possible acoustico-lateralis perception was distinguished. As light diminished, deflection from the vertical grill of tubing alone fell to insignificance. With polished brass chain inserted, the highly significant response was maintained. The pressure or bow wave created by the chain or tubing in moving water was, therefore, not the effective agent.

Structure and Photomechanical Responses of the Retina

In the vertebrate eye visual acuity and sensitivity are mutually exclusive (Walls, 1942). The fine-grained perceptive power of the light-adapted eye relying predominantly on cone vision is replaced by the additive system of rod vision in the dark-adapted eye where numerous individual endings sum their responses to stimulate individual nerve fibres. Hence, acuity must be sacrificed for sensitivity.

The salmon eye is not distinguished by specializations within the general structural plan of the vertebrate eye. Oculomotor muscles appear to relate almost entirely to the more primitive function of equilibrium response. The iris is non-contractile. With the possible exception of the peripheral portion of the retina, rods and cones are uniformly distributed without the localized cone concentration of a fovea (Brett and Ali, 1958). The lack of a well ganglionated nerve fibre layer is indicative of average acuity. It is obviously a versatile eye, serviceable for day and night vision without the highly developed resolving powers and mobility for selecting and following moving objects which characterize vertebrates possessing foveated retinae.

In the guiding experiments, at the time of peak migration, light was changing rapidly with the onset of nightfall. It was, therefore, of interest to know the state of dark-adaptation and the photomechanical rate of change. Unlike other sensory endings, there is an obvious cellular change related to stimulus intensity in the receptor organ (retina) which can be examined histologically. The slow rate of contraction of the visual endings and movement of masking pigments in the encasing epithelium is not distorted by rapid killing and fixing techniques. It was discovered that dark-adaptation took 55–60 minutes for completion whereas the reverse process only took one-half that time (Brett and Ali, 1958). By sampling during migration, retinal sectioning revealed that the process of change from light- to dark-adaptation characterized the period of peak migration within the river. Earlier activity in the lake to reach the river would be with a light-adapted eye. In the case of pink and chum salmon fry emerging from gravel beds for nocturnal movement, the commencement of migration coincided with advanced dark-adaptation. The fairly precise timing of the latter may well be triggered by appropriate retinal responses.

The reduced acuity with onset of darkness could account for the partial decrease in avoidance of obstacles such as the curtain of chain. Reduction in the cohesion of the school could also account for the change. Nevertheless, adequate vision appeared to characterize even the latest periods of migration.

Light and Feeding Ability

The threshold level of visual response also became a significant question in the problem of guiding. Flood lighting of stream areas not only involved behavioural changes but exposed the concentrated fish to unusually high predation. That only a small amount of light was needed for guiding was apparent from the effective but diminished level of deflection achieved late at night without supplementary lighting. Laboratory tests based on the ability to feed at various ight levels were conducted on cultured young coho during the winter. These are here reported for the first time.

Using *Daphnia*, screened for fairly uniform adult size, fish were always fed at the same time of day with an accompanying sound stimulus produced by tapping on the side of the experimental tank. The latter was a blackened battery jar, covered with a ground-glass top, and drilled to permit exchange of water as well as remote feeding through a funnel (Fig. 2). Directly above the tank a light box with a fine iris-diaphragm could be lowered or raised to the ceiling thereby altering the light intensity without changing the source for any one series. The use of a single source did not prove to be possible because of the immense range of eye sensitivity of the fish. By using Mazda bulbs of 15 and 150 watts most of the range was covered. A final test to see if glare could interfere with rate of feeding involved a Sylvania 1000-watt flood. To produce

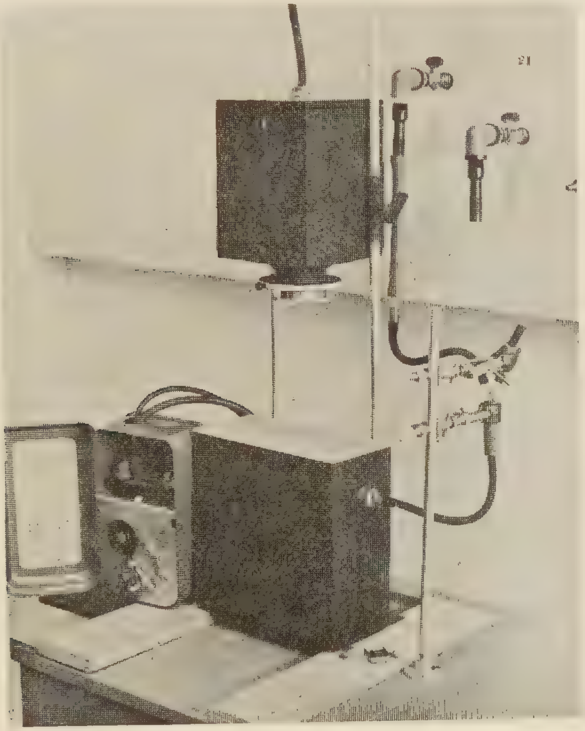

FIG. 2. Apparatus for studying the ability of young coho to feed on *Daphnia* under various light intensities. The light box with iris disphragm is shown clamped in one position above the black battery jar containing the fish. The funnel at right was used for remote feeding. Set up in a darkroom, the time-switch at left turned on a preselected light intensity, two hours before a test.

even dispersal, a second ground-glass plate was placed a few inches from the light source (not shown in Fig. 2).

Measurements were made with a Photovolt photometer (Model No. 210) filtered for the "human observer", this being the nearest general commercial equivalent to the unspecified spectral sensitivity of the salmon eye. By taking closeup readings for those intensities which approached the minimum sensitivity of the photometer (0.001 ft-c) it was possible to calculate the lower intensities illuminating the test jar at greater fixed distances.

The foot-candle unit used is not a particularly desirable one since it implies a standard source of given spectrum, providing a measure of luminous intensity. Filtered mainly for wavelengths from 450 to 600 mμ which includes the sensitive blue-green range of fish, the meter read approximately 0.003 ft-c in bright moonlight.

The plateau of learning to feed on the *Daphnia* reached about 95 consumed out of 100 available in a period of 5 minutes. A coarse meshed net was used to remove the fish after the exact time interval, leaving the balance of *Daphnia* for subsequent counting. Observations under normal light revealed that the fish selects the prey, manoeuvers, darts, captures and swallows. This staged process continues in rapid succession. It did not appear to be proportional to numbers until the majority were eaten.

The first indication of interference from insufficient light on the rate of feeding occurred at 0.01 ft-c (Fig. 3). From this level a progressive drop to near inability occurred at a rate of decrease almost proportional to the logarithm of the light intensity. A feeding rate of one-half the maximum was still possible at 0.0001 ft-c, with an extinction level close to 0.00001 ft-c. Bright moonlight would be about 300 times this intensity. No feeding was possible in complete darkness, despite the fact that the fish must have been bumping into the *Daphnia*.

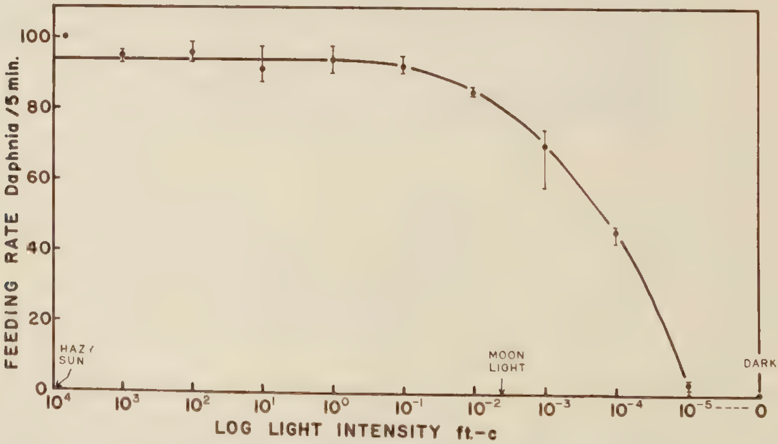

FIG. 3. Relation between the feeding rate of trained young coho salmon and logarithm of light intensity, measured with a Photovolt photometer, Model No. 210, filtered mainly for wavelengths from 450 to 600 mμ. Hazy sun and bright moonlight levels are indicated. Each point is the average of three to five determinations with range shown (except highest and lowest points).

At the other end of the light scale an intensity of 9000 ft-c had no effect on feeding rate, despite the glare. This signifies a capacity to meet lighting conditions which differ in intensity by a factor of over 1×10^9. Obviously the salmon eye is highly adapted to a wide range of intensities.

A remarkably similar type of experiment has been reported by Jones (1956) using the minnow *Phoxinus*. Unlike the young salmon these fish were able to feed on *Daphnia* in the dark. Significantly improved feeding rates occurred with light intensities ranging from about .001 to 0.0001 meter-candle (1 ft-c = 10 m-c approximately) which is in close agreement with the salmon responses.

Celestial Orientation

Following the remarkable developments revealed in the migration and homing behaviour of birds which show an ability to use light patterns from the sky coupled with some form of accurate time sense to maintain persistent geographic directions (reviewed by Kramer, 1959; Sauer and Sauer, 1960; Verwey, 1958), other investigators have examined and found similar phenomena in vertebrates including turtles (Gould, 1957) and fish (Hasler *et al.*, 1958; Braemer, 1959; Hasler and Schwassman, 1960). Since salmon make long migrations under conditions in which landmarks are either inappropriate, distant or deep, at times displaying highly directed and seasonally timed movements, the question of celestial orientation invited attention.

Using apparatus and methods similar in concept but modified in design from those for birds, the first step was to decide what stage to investigate and what behaviour of captive salmon could be used to provide experimental evidence on the directional preferences.

Young sockeye in the early spring after a year or more of residence in a lake annually make their mass exodus in a diurnally pulsed migration. The timing of the pulse correlates with the rapidly changing light conditions surrounding dusk and dawn, the dusk movement being the more pronounced. In captivity when held outdoors in a circular tank some of the fish show increased fluttering against the transparent face at these particular times and will also hold position with the body axis pointing in one direction much as birds perform what is termed "migration restlessness", oriented in a given direction from a perch in a cage.

An intensive study of this stage in young sockeye and the associated behaviour patterns has been in progress during the migration period in the large multi-basin waters of Babine Lake (174 sq. miles), combining ecological studies (Johnson, 1956, 1958, 1961) with orientation experiments (Johnson and Groot, 1961). By observing with the unaided eye or with field glasses from high above the lake, and plotting directions by means of a transit, numerous schools can be seen moving on a parallel course down-lake, well dispersed from shore and not deviating from a compass direction in relation to small irregularities of shoreline and bottom configuration. Preliminary lake surveys synchronized with migration observations indicate the selected path to be independent of surface drift currents (wind produced) and temperature isotherms. Achieving an average track-made-good of 4–5 miles per day and moving from opposing directions of the Y-shaped lake for distances of 50–70 miles, the young migrants display excellent oriented migration with an *apparent* sense of direction and geography, leading to the outlet goal. Definite exceptions have been recorded and only the surfacing schools can be tracked. However, the large number of readily observed schools on a calm evening make it unlikely that the major phenomenon is not being witnessed.

Orientation experiments have been performed on single fish in either octagonal or circular plastic tanks shielded to permit vision of the sky only, except in some comparative studies where the horizon was left visible. Observations have been made between noon and midnight, the observer lying underneath the transparent tank on a curtained platform recording positions, directions, swimming movements and behaviour activities. Between observations the platform was rotated clockwise or anticlockwise to eliminate possible cueing from inside the tank.

At the present stage of testing and analysis, with various experiments of a critical nature yet to be performed, a number of statements can be made, concluding with a general hypothesis. These are:

1) With vision of the sky only, both before and after sunset, a directional tendency can be maintained within a limited range of compass points.

2) Complete cloud cover or obscuring the sky experimentally generally produces random directions or fixed positioning related to some internal feature of the tank. Some remarkable exceptions exist with directions maintained despite complete overcast and a sheet covering the tank.

3) Samples tested from different points in the same lake and from different lakes show preferred directions which are mostly appropriate to the path of migration leading directly to the lake outlet.

4) There is a diurnal and seasonal shift in the preferred direction which in some stocks follows a pattern of change necessary for the correct migration route.

5) The persistence of the direction finding, independent of the changing position of the sun or other celestial phenomena, requires a diurnal rhythmic sense equivalent to an internal clock.

To explain such directed migration, one of the major unanswered questions is that of position finding. It is not enough to select a compass direction, the direction must be geographically appropriate. Also, the observed path of migration does not show seasonal changes in direction when passing a given point in the lake, and mystery surrounds those exceptional fish which persist in a given direction experimentally despite obscured skies.

To conclude it is hypothesized that celestial phenomena are used in the time-compensated orientation of migrating sockeye which, by an unknown inherited mechanism, provides a direction appropriate to the particular escape route from the lake.

This hypothesis requires that each stock has separately evolved the necessary geographic response and that position finding is a property of the adult which must return unerringly to the correct area of the lake so that the young will react appropriately. While there is evidence that the adults do achieve such accuracy, this phenomenon is not as difficult to conceive as that of inheriting the right geographic responses since the adult fish return on a course in which previous imprinting and learning can play important roles.

It should be noted, however, that Pardi (1960) discovered by raising the eggs from distinct geographic populations of amphipods that appropriate directional tendencies could be inherited. Such an experiment would be pertinent to the question for young sockeye.

GENERAL DISCUSSION

Many authors have added to the description of Pacific salmon migration (Chidester, 1924; Davidson *et al.*, 1943; Hoar, 1954, 1958) facilitated by the relatively accessible nature of many of the freshwater phases, leaving aside the less accessible aspects of ocean movement and behaviour. Even these are yielding descriptively little by little through the work of International Commissions and their contributing agencies. It has been tempting to speculate on the nature of migration, but few have set out to properly analyze the basis and formulate working hypotheses.

In North America two authors and their associates stand out in regard to recent theories on salmon migration, namely Hoar (1954, 1958) and Hasler (1954, 1957). The former has dealt with the mechanisms and possible evolution of behaviour in the juvenile or fry stage, considering the effect of such environmental factors as light, temperature, current and salinity. River migration at this early stage is related to nocturnal changes in behaviour which result in rising from the stream bottom, increased activity, moving into faster water coupled with displacement or active swimming downstream. Daily stream migration in small rivers is terminated with the coming of dawn when cover is sought. McDonald (1960) has shown that the daily period of migration is extended when far from the site of emerging or if waters are turbid.

The sensory basis and effective cues are left to speculation in which considerable reduction and even loss of visual contact at night is one of the main suppositions, employing the term negative phototaxis, yet, as has been determined experimentally, salmon can avoid objects late at night as underyearlings, continue to navigate with the possible aid of celestial phenomena as smolts, and move upstream all night as adults (Ellis, 1961). Downstream migration is classified as negative rheotaxis; however, should the fish be actually swimming downstream then water must be streaming from head to tail (positive rheotaxis ?) with visual images, if present, flashing across the retina.

The behavioural analysis of migration differs in its approach from that of Hasler who, as mentioned earlier, has continued to seek the sensory basis of homing by considering olfactory and visual stimuli. A variety of fish have been investigated. In the white bass, *Roccus chrysops*, by the use of ingenious eye caps permitting sky vision only, homing of displaced nesting fish was shown to be possible through sun-compass orientation maintained by supposing an internal clock, with final location thought to be by local geographic knowledge (Hasler *et al.*, 1958). Various species of centrarchids and cichlids have been readily trained to use the sun as a directional cue (Hasler and Schwassman, 1960). Gunning (1959) demonstrated that long ear sunfish (*Lepomis megalotis*) required an intact olfactory organ to return to a home range, whereas blinding did not impair this ability. The learning of topographical characteristics of an area mediated by vision is apparent in the orientation and accurate jumping of the goby (*Bathygobius soporator*) from one tidal pool to another (Aronson, 1951).

Pacific salmon, as has been shown, possess sufficiently adequate visual and olfactory senses to be able to employ these effectively in homing. But does even the obvious nature of the environment support the possibility? Odours *alone* have been placed in doubt as an effective *distant* agent by virtue of homogeneity and/or discontinuity. Vision can be disposed of in many instances by the simple fact that heavy turbidity effectively blinds other than light-dark sensitivity, but migration continues in the glaciated and muddy waters of many a salmon river. Griffin (1953) has commented that "the solution (to migration problems) may be expected to stem from more thorough investigation of the environmental cues actually available to the animals" and that "new types of behaviour patterns are to be expected more than new types of sensory windows".

At this point it is profitable to examine briefly some of the environmental factors such as Hoar and Hasler have introduced and to consider their directional qualities in terms of perception and orientation[5].

LIGHT. Stimulating the eye, pineal organ and certain pigment cells directly, light provides information on movement, form and colour of objects near and far. In its daily cycle it produces or harmonizes cellular rhythms which phase activity, possibly "corrects" an internal clock, and provides for local intensity differences producing shadows used as cover. With high transmission qualities through air and relatively so in water, it is differentially absorbed by many bodies, being reflected and refracted at interfaces. Its high frequency provides the phenomenal beaming qualities which make it the ideal distant, directional environmental factor, provided particulate matter does not interfere. Because of the discrete path of light, sensory receptors can occur close together yet be useful in accurately localizing objects, both in regard to direction and distance.

CURRENT. The movement of water may be laminar or turbulent involving eddy currents, waves and shearing at density interfaces. The sensory systems of sight, lateral line, inner ear and touch, individually and collectively can be concerned in detection. In the presence of adequate light the fixing of retinal images by upstream swimming results in orientation to current. So-called "distant touch" provided by the lateral line apparently serves to identify the hydrodynamic distortions produced by bottom irregularities and moving objects. When in tactile contact with fixed objects direction of water movement is also provided. In this way, the immediate course and characteristics of water are detected. Localization of relatively near objects is afforded, and, in so far as points of fixed reference are present, current identifies the continuous though irregular path of water which may traverse great distances. Orientation to a distant goal is not afforded directly, but the transport of dissolved materials can include distinctive components.

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[5] See references in: *Symposia Soc. Exp. Biol.*, **4**, 1950; *J. Fish. Res. Bd. Canada*, **11**(2), 1954; The Physiology of Fishes, II, Academic Press, 1957.

SOUND. Vibrations or pressure pulses are registered by the otolith organs of the inner ear in which the distinction of pitch or tone may be enhanced by internal resonators such as the swim bladder. The lateral line and tactile skin endings have been variously described as sensitive to low frequencies and intense levels. Since the upper range of audibility in fish which lack a Weberian apparatus has not been reported to exceed about 5000 cycles/sec, and optima fall in the vicinity of 1000 cycles/sec, the desirable beaming qualities of high frequency sound are not reached. Excellent transmission in water would serve to alert fish to the presence of a source from considerable distance but direct localization would be difficult unless close at hand where intensity differences might be employed.

CHEMICALS. Dissolved organic and inorganic substances can serve to stimulate olfactory, gustatory, cutaneous and possibly mouth or gill surfaces when salinity involves chloride secreting cells. As stated earlier recognition of soluble fractions arising from animate or inanimate sources is possible but unless near the immediate source localization is impossible by reason of the non-directional or discontinuous path.

TEMPERATURE. Cutaneous thermal receptors in teleosts appear to be the sensory system responsive to temperature gradients. Absolute temperature levels may be determined by the basic rate of impulses discharged by the lateral line. Although unquestionably affecting the frequency of movements of active fish, there is still considerable question of discrimination in unconditioned fish, particularly in a suitable thermal environment not pressed by disturbing extremes. It is sufficient to note here that water masses might be identified but not the direction of the source except by crossing the usually irregular isothermal lines. The possibility of thermal orientation outside the steep horizontal gradients imposed in laboratory studies remains open to speculation. Finally, temperature is known to alter responses to currents and to light (Keenleyside and Hoar, 1954; Andrews, 1952).

This accounts for the main pathways of environmental cues, except those from the direct pressure of depth, from gravity and acceleration, providing labyrinth responses, and from electrical fields which can cause acute cellular reactions. The limited compilation is presented to bring illustration and emphasis to the multiple role and interplay of sensory systems. Unless very near to the source or proceeding on a recognized topographical path no *one* factor can provide for directed migration. Sequences, interdependence and substitution of environmental cues likely come into play. Consider odour and current. Without prevailing transport the source of the odour cannot be localized from a distance. This is recognized in the attraction of insects to mate or prey. Kalmus (1958) records that "on catching the scent of the female the (male) moth starts to fly straight into the wind . . . his sole cue to location of the distant female is the direction of the wind" which is apparently dependent on sight since "on a completely dark night the moth cannot find its way toward a scent". R. H. Wright (personal communication) has further shown experimentally that "fruit flies in flying up-wind to the source of an attractive scent depend on their view of the ground to determine the wind direction, and become confused if moving spots of light are projected on the ground under them". Without prevailing wind, dogs can only track an animal by following the irregular path of localized scent temporarily emanating from fixed positions.

By analogy it is reasonable to suspect that homestream odours excite salmon to move against a current, which in the absence of good visual contact arising from turbidity, may well be recognized by turbulence cues. The sequence becomes excitation by odour in which detection of highly dilute levels is *aided* by discontinuities, response to current by retinal detection with substitution by acoustico-lateralis identification as an alternate response mechanism.

Movement through relatively quiet water such as sockeye smolts experience in lakes becomes somewhat more understandable in the knowledge of potential orientation by celestial reference, but appropriate alterations of course and changes in behaviour indicate an interaction and sequence of sensory perception in which only some of the essential fragments of the picture can be recognized.

Confining our attention to subsurface perception it can be deduced that two major organ systems remain unaffected by turbidity—the olfactory and the acoustico-lateralis systems. Tactile senses may play a periodic role, but observations preclude this as a useful migratory reference system since contact is rarely a feature of the free swimming smolt or adult, but could be of significance in the fry which nocturnally emerge from gravel beds and return to this refuge during the early phase of downstream movement.

The subtle, not to say remarkable, forms of sensory development which are recognized such as echo-location in bats, cetaceans and some birds, the use of polarized light by a variety of invertebrates, the ability of bees to translate sun-compass directions into equivalent gravity vectors, and of ants to sense shapes from odours, are examples of achievement employing well known sense endings but of earlier unsuspected performance (von Frisch, 1950; Carthy, 1956). In this respect there appears to be a relatively large gap in our understanding of the acoustico-lateralis system of fish. It is in the area of hydrodynamic sense, the apparent blind "vision" of fish, that research is likely to be doubly rewarding.

CONCLUSIONS

Despite the scattered nature and somewhat unrelated lines of research which characterize the literature on olfactory and visual perception in salmon it is apparent that some general conclusions can be drawn.

The innate ability to perceive highly dilute odours and to react selectively by excitement behaviour supports the view that olfaction can play a major role in near and distant perception. *Distant* odour perception, however, is unlikely to be directive, and requires the support of one or more additional cues to be effective in identifying the source.

Vision plays a dominant role in many of the salmon's activities, and, although subject to inevitable loss of acuity at night, appears to be sensitive enough to permit registering many environmental features. Celestial orientation is a characteristic of young sockeye and is likely instrumental as a visual cue in the highly directive lake migration. Innate ability to maintain a sun-compass direction indicates the presence of a rhythmic sense diurnally timed.

Persistent upstream migration in adults, despite turbid water, and an obvious ability to perceive subtle hydrodynamic features points to the well-developed use of the acoustico-lateralis system possibly supported by cutaneous and proprioceptive responses. These particular sensory mechanisms require increased attention and exploration in order to interpret many features of behaviour.

Speculation on the sensory basis for migration must take into account physical properties of the environmental cues and the limitations imposed by sensory physiology including thresholds, fatigue, suppression and interference. There is a great need for detailed study of the sensory mechanisms in general.

ACKNOWLEDGMENTS

We are indebted to Professor P. W. Gilbert of Cornell University for his suggestion and invitation to write this paper for presentation at a symposium on "Factors affecting the behavior of predaceous marine fishes, especially sharks", delivered at the Tenth Pacific Science Congress.

During the studies on visual sensitivity of young coho, Mr D. B. Sutherland diligently attended to all technical matters, and Dr M. A. Ali, then a graduate student at the University of British Columbia, assisted in some of the experimental work.

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Movements, Growth and Survival of Marked and Tagged Lobsters Liberated in Egmont Bay, Prince Edward Island[1]

By D. G. Wilder

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

The average straight line distance between release and recapture points of 253 tagged lobsters free 10 to 12 months was 7.3 nautical miles (13.5 km). Carapace-length growth increments per moult among 870 punch-marked lobsters recovered from the fishing grounds were independent of size and averaged 0.47 inches (11.9 mm) for males and 0.42 inches (10.7 mm) for females. Weight increments per moult varied from 4.0 to 7.5 ounces (113–213 g) for males and from 3.3 to 5.4 ounces (94–153 g) for females. Of the males, 17.8% moulted twice; of the females, 7.4%. Survival over a 10-month period was estimated to be 76.4%.

INTRODUCTION

The lobster fishing season in the northern half of Northumberland Strait between Prince Edward Island and New Brunswick is August 10 to October 10. With minor changes this so-called "fall" season has been in effect for more than 20 years. In the remainder of the southern Gulf of St. Lawrence the season is May 1 to June 30.

As a general rule in the southern Gulf moulting occurs during July, August and September (Templeman, 1936). Consequently, many of the lobsters caught during the fall season have recently moulted and are soft shelled. Such lobsters are difficult to store and ship alive, particularly in the warm water and high air temperatures that prevail throughout most of the season (McLeese, 1956).

The fall-season area, surrounded by the spring-season area, makes enforcement of the fishery regulations extremely difficult. Lobsters caught illegally during August and September in the spring-season area can be readily disposed of if they reach the nearby fall-season area undetected. Fishermen, particularly those from the spring-season area who like others are restricted by law to one fishing season a year, are often inclined to fish the fall season when the lobsters can be caught with little effort (McLeese and Wilder, 1958). To avoid these difficulties one season throughout the southern Gulf has been suggested. This has, however, been opposed by fall-season fishermen who have contended that lobsters migrated from their area and were too scarce in the spring to support a fishery. In 1954 the fishermen of Abrams Village on Egmont Bay, P.E.I., requested a study of the movements and growth of lobsters in that area.

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[1] Received for publication September 5, 1962.

J. Fish. Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

METHODS AND MATERIAL

To learn something of movements in the Egmont Bay area, 998 female lobsters were tagged with conspicuous monel-metal, serially numbered carapace tags (Wilder, 1954) and liberated just after the 1954 season closed on October 5. On October 6, 498 were liberated $1\frac{1}{2}$ to 2 miles (2.8 to 3.7 km) WNW of Abrams Village wharf at a depth of 4 fathoms (7.3 m) as shown in Fig. 1. A further 500 were liberated October 8, 1954, at 8 fathoms (14.6 m), $4\frac{1}{2}$ to 5 miles (8.3 to 9.3 km) west of the wharf. A reward of 25 cents was paid for the return of each tag. The carapace length of these lobsters, measured parallel to the mid line from the posterior margin of the eye socket to the posterior margin of the carapace, ranged from 3.0 to 3.8 and averaged 3.3 inches (84 mm).

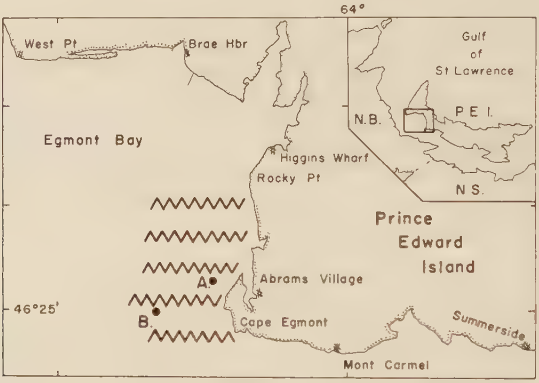

FIG. 1. Points where marked and tagged lobsters were liberated in Egmont Bay, Prince Edward Island. **A** — 6,716 marked and released September 15 to October 4, 1954, and 498 tagged and released October 6, 1954. **B** — 500 tagged and released October 8, 1954. ΛΛΛΛΛ 100 tagged and released along each line August 4 to 6, 1955.

To estimate growth, lobsters were marked by punching $\frac{3}{16}$-inch (5 mm) diameter holes through two sections of the tail fan as described by Wilder (1953). A standard leather punch, somewhat modified as shown in Fig. 2, was used. To facilitate cutting and to reduce breakage of the tail fan, 7 sharp teeth were filed in the cutting edge of the punch tube. The anvil of the punch was removed and a tongue of steel, with a hole to allow passage of the punch tube, was welded to the lower jaw of the punch. In marking, the tail fan was inserted between the tongue and the lower jaw. The tongue held the tail fan down and so facilitated withdrawal of the punch tube.

From September 15 to October 4, 1954, 6,989 sub-legal (less than $2\frac{1}{2}$ inches (63.5 mm) carapace length) lobsters were measured with specially designed brass calipers graduated in thirty-seconds of an inch (0.8 mm). Carapace lengths rather than total lengths have been generally used by Canadian workers over the past 10 years because of greater accuracy and convenience and because minimum size limits are based on this measurement. The rather unconventional

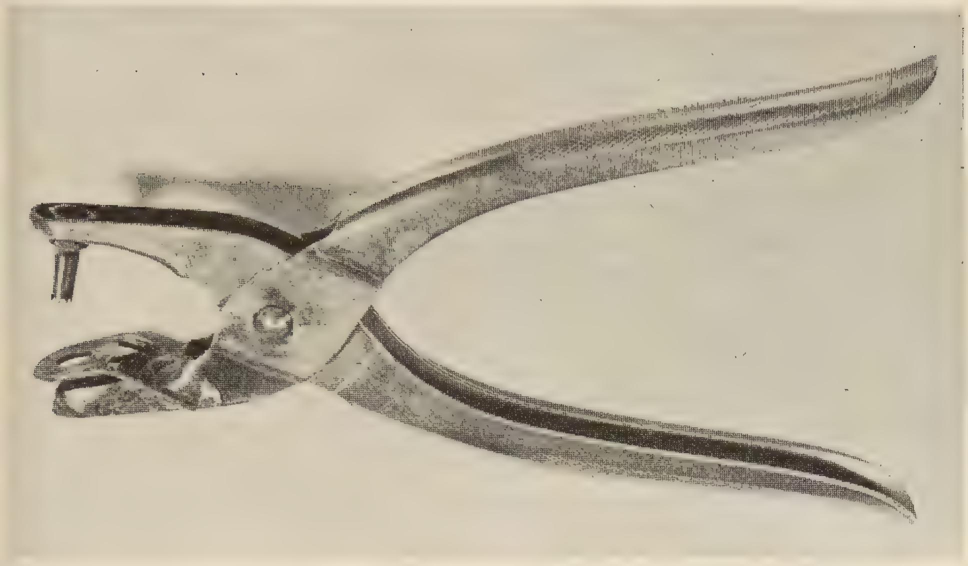

FIG. 2. Leather punch modified by filing teeth in punch tube, removing anvil and welding tongue to lower jaw.

unit of measurement was used to facilitate evaluation of size-limit changes which have been as small as one-sixteenth of an inch (1.6 mm). The lobsters were marked distinctively in three length-groups, the mid-points of which were $2\frac{3}{16}$ inches, $2\frac{5}{16}$ inches and $2\frac{7}{16}$ inches. At the time of liberation, 273 of the marked lobsters were found dead or mutilated and were discarded. The remaining 6,716 were liberated, weather permitting, the day they were marked. All were released $1\frac{1}{2}$ miles (2.8 km) WNW of the Abrams Village wharf, where the tagged lobsters were liberated October 6, 1954. The marks used and the numbers of each sex in each size-group were as follows:

	Carapace length mid-point		Tail fan sections[a] marked	Numbers released		
Size-group	inches	mm		Males	Females	Total
I	$2\frac{3}{16}$	55.6	2 and 3	254	332	586
II	$2\frac{5}{16}$	58.7	2 and 4	909	1,093	2,002
III	$2\frac{7}{16}$	61.9	3 and 4	2,119	2,009	4,128
				3,282	3,434	6,716

[a] Numbered from left to right. Sections 1 and 5 not used as they are jointed and more fragile, especially in such small lobsters.

Marking was delayed as long as possible so that few of the marked lobsters would be recaptured during the remainder of the season. However, 193 marked lobsters were found among the sub-legal lobsters landed by special arrangement for marking. These were promptly returned to the water. Although only three small boats were fishing near the liberation point, the marked lobsters apparently moved about enough to permit prompt recapture of appreciable numbers by other boats. Undoubtedly some of these marked lobsters, particularly the larger ones, were landed and sold by accident or intent during the 1954 season. No data are available to permit an actual estimate but observations suggest that not enough were involved to affect survival estimates seriously.

No rewards were offered for the return of punch-marked lobsters as it was felt that this could lead to falsification of marks, inconsistent search for the rather inconspicuous marks and dissatisfaction regarding payment for doubtful cases. Instead, a crew of specially trained technicians and fisheries wardens examined commercial catches as they were landed. Four men stationed full time in the Egmont Bay area examined 235,000 pounds (107,000 kg) of lobsters, or about 42% of the catch, from Cape Egmont to but not including West Point. From West Point to North Point two part-time observers examined 27,500 pounds (12,500 kg) and from Mont Carmel to Summerside four part-time workers looked through 42,600 pounds (19,400 kg). On the New Brunswick side of the Strait one full-time worker examined 100,000 pounds (45,500 kg) from Cape Tormentine to Pt. Sapin.

To calculate the number of marked lobsters that survived, an estimate of the fraction recaptured during the 1955 season was required. This was obtained by liberating 500 tagged, legal-sized lobsters just before the start of the 1955 season. These lobsters which were obtained by pre-season fishing in Egmont Bay were measured, tagged with carapace tags and released within a few hours of capture. They ranged from 2.5 to 4.3 inches carapace length and averaged 2.9 inches (74 mm). They were distributed over the Abrams Village fishing grounds in five lots of 100 as shown in Fig. 1.

MOVEMENTS

In assessing movements, only the lobsters liberated in October 1954 are considered in detail. Unlike those tagged in 1955, these were released at two specific points so that more accurate measurement of movement was possible and they were at liberty long enough (10-12 months) for seasonal movements to occur. A basic difficulty in the study of long-term lobster movements is the loss of external tags at moulting, particularly among immature lobsters and mature males which moult more often than mature females.

From observations of egg-bearing females and from the width of the second abdominal segment, Templeman (1944) concluded that in the Egmont Bay area the smallest mature females were about 17.5 cm total length (2.3 inches carapace length) and only about half the females were mature at a length of 23.8 cm (3.2 inches carapace length). Measurements of sample catches at Abrams Village throughout the 1946 season showed that of 4,514 legal-sized females, approximately 90% were less than 3.2 inches carapace length. Although males mature at smaller sizes than females (Templeman and Tibbo, 1945) it is clear that a large fraction of the legal-sized lobsters in the Egmont Bay area are immature. Most such lobsters tagged in October would be expected to moult and lose their tags before the next fall season opened on August 10. In order to have appreciable numbers of tags retained until the season reopened, only females of 3 inches carapace length and over were tagged. Most of these would be mature and would be expected to lay eggs early the next summer in the old-shelled condition (Templeman, 1940). Such lobsters could be expected to retain their tags for more than a year.

None of the tagged lobsters were reported from the spring-season area either the following May and June or during the 1956 season. To be caught in this area they would have had to move at least 30 nautical miles (56 km) in a southerly or 40 miles (74 km) in a northerly direction in 8 to 9 months.

Of the 998 tagged lobsters released, 253 were returned during the 1955 season—157 (62%) by Prince Edward Island fishermen, the remainder by New Brunswick fishermen. Their approximate recapture points are shown in Fig. 3. The peculiar pattern of returns off West Point, Abrams Village and Cape Egmont is to a large extent the result of inaccurate reporting by the fishermen. The straight line distances between liberation and recapture points to the nearest nautical mile were as follows:

Miles	Number	Miles	Number	Miles	Number
0	5	9	9	18	0
1	9	10	8	19	0
2	9	11	16	20	3
3	36	12	22	21	1
4	25	13	14	22	1
5	29	14	7	23	0
6	22	15	0	24	1
7	24	16	2	25	2
8	6	17	2	Total:	253

The average straight-line distance between the points where the lobsters were liberated and where they were recaptured 10 to 12 months later was 7.3 nautical miles (13.5 km). No lobster was reported farther than 25 miles (46 km) from its liberation point and 95% were reported within 15 miles (28 km). Egmont Bay boats (West Point to Cape Egmont) returned 149 (59%) of the tags recovered.

It is possible, of course, that relatively large females are more or less mobile than the legal-sized stock as a whole. Templeman (1935) presented rather limited data indicating that mature females moved farther than mature males. Simpson (1961), on the basis of considerably more tag returns, concluded there was virtually no difference in the movements of male and female *H. vulgaris*. Our extensive tagging data (Wilder and Murray, 1958), although not yet analyzed in detail, have shown no clear relationship between size, sex and movements within the legal-size range.

Only the general area of recapture is known for the punch-marked lobsters. The 870 recovered during the 1955 season do, however, show the same pattern of movement as the tagged lobsters. Over 94% of the marked lobsters recovered were recaptured by Egmont Bay boats. None were found north of Richibucto Cape, N.B., and West Point, P.E.I., among 29,000 pounds (13,200 kg) examined and none south of Lower Cape Bald, N.B., or Mont Carmel, P.E.I., among 53,000 pounds (24,100 kg).

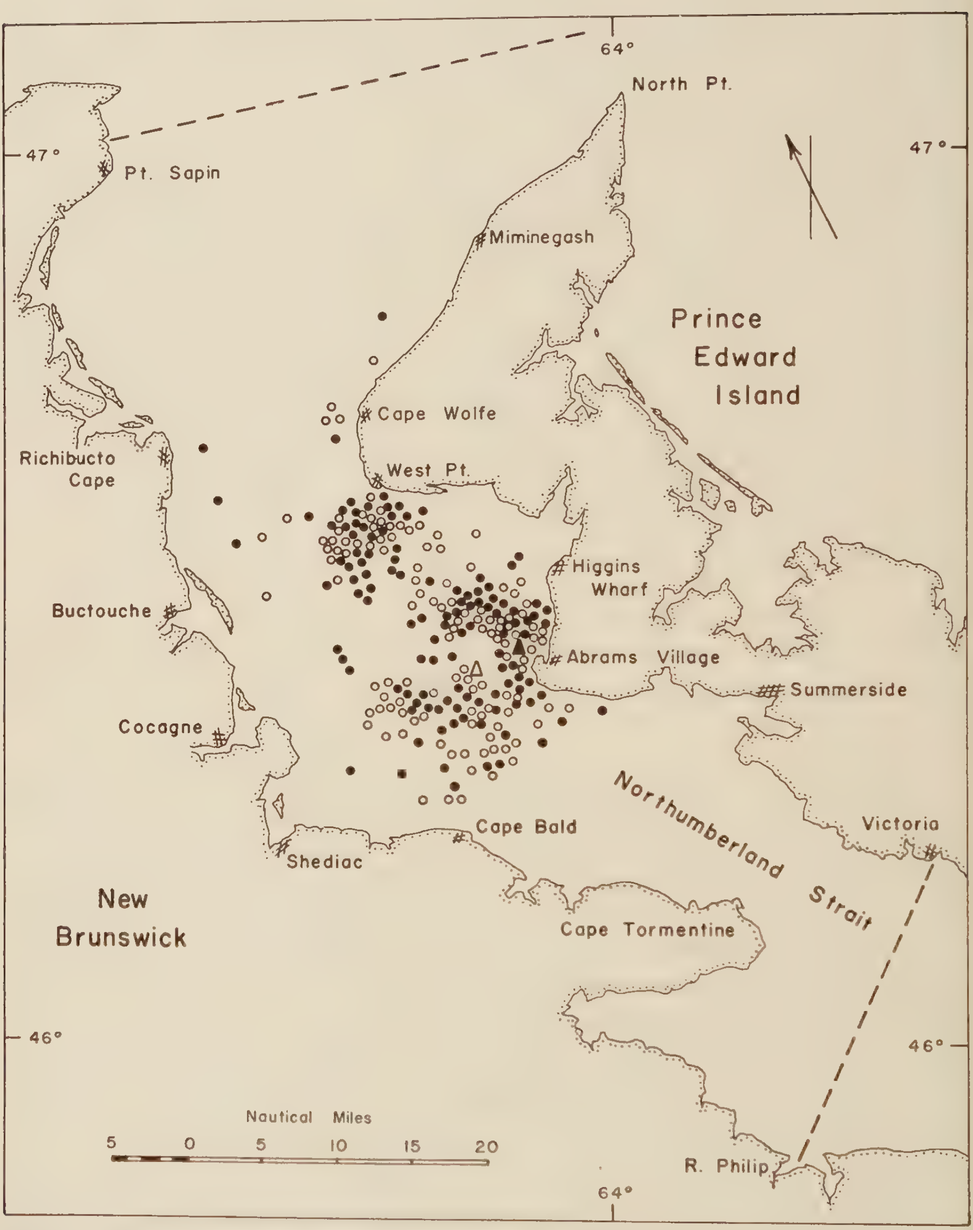
64°
North Pt.
47°
Pt. Sapin
Miminegash
Prince Edward Island
Cape Wolfe
Richibucto Cape
West Pt.
Higgins Wharf
Buctouche
Abrams Village
Summerside
Cocagne
Northumberland Strait
Cape Bald
Victoria
Shediac
New Brunswick
Cape Tormentine
46°
Nautical Miles
5 0 5 10 15 20
R. Philip

FIG. 3. Northumberland Strait fall lobster season area. The two triangles show where tagged lobsters were released October 6 and 8, 1954. Recoveries during the fall season, August 10 to October 5, 1955, from offshore liberation shown by open points; from inshore liberation by closed points.

GROWTH

From August 4 to 6, just prior to the 1955 season, 15 marked lobsters were recovered while fishing for lobsters to tag. A further 855 were found during the August 10 to October 5 season to bring the total to 870. All but one had moulted. When the carapace lengths were averaged by 2-week periods, as in Table I, a definite increase was noted after the second 2-week period, indicating a second moult in early September. On the basis of shell condition, Templeman (1936) concluded that in this general area most lobsters from 15 to 23 cm total length (2.0 to 3.1 inches carapace length) moulted in July and again in September. The sharp rise in commercial landings (Table VI) in early September is also indicative of a second moult at that time. The carapace length distributions of the marked lobsters recovered are recorded for each sex by size-groups in Table II.

TABLE I. Average carapace lengths in inches (1 inch = 2.54 cm) of marked lobsters recovered by 2-week periods during 1955 season. Number of specimens in parentheses.

Period	Group I	Group II	Group III
Aug. 10–Aug. 23[a]	2.7 (53)	2.8 (170)	2.9 (405)
Aug. 24–Sept. 6	2.8 (13)	2.7 (44)	2.9 (75)
Sept. 7–Sept. 20	2.8 (9)	3.2 (28)	3.3 (34)
Sept. 21–Oct. 5	3.0 (4)	3.2 (3)	3.4 (32)

[a] Includes 15 lobsters caught Aug. 4–6, 1955.

From previous marking experiments and from the literature, Wilder (1953) presented evidence that the maximum growth per moult among lobsters of this general size range was of the order of 20% for both sexes. Groups I and II, where lobsters moulting once and twice seem most clearly separated, suggest maximum growth per moult of 18 and 19 thirty-seconds of an inch (14 and 15 mm) or 25.7%. This figure, used as a criterion to distinguish single and double moults, indicates that of 760 recovered during the first half of the season, only 18 (2.4%) had moulted twice. Of 110 found during the last half of the season, 95 (86.4%) had moulted twice. Even though most of the lobsters were immature when marked, the males moulted more frequently. Of 466 males, 83 (17.8%) moulted twice; of 404 females, only 30 (7.4%) did so. The size distributions of lobsters recovered are plotted in Fig. 4.

In Table III the average carapace lengths attained after one moult are compared with the group mid-points when marked to calculate growth during the first moult. Similarly the lengths attained after one and two moults are compared to determine the growth during the second moult. A comparison of the average lengths of all lobsters recovered with the group mid-points when marked gives growth over the 10- to 12-month period. Growth of Group I lobsters at the second moult was relatively low. Since these averages are based on only a few recoveries, nothing more than experimental error may be

TABLE II. Number of lobsters released at Egmont Bay, P.E.I., September 15 to October 4, 1954, and recovered August 4 to October 5, 1955, according to carapace length and sex. Length measurements in thirty-seconds of an inch (0.8 mm).

	Group I		Group II		Group III	
Length when marked—mid-point:	70		74		78	
Sex:	♂	♀	♂	♀	♂	♀
Number marked:	254	332	909	1,093	2,119	2,009
Length when recovered						
78	...	1	...	...	1	...
79	...	1	...	...	...	...
80	1	3	...	...	...	...
81	1	3	1	...	...	...
82	1	5	1	4	...	...
83	5	6	1	2	...	...
84	4	4	5	14	...	...
85	5	8	2	8	1	2
86	6	3	9	18	2	4
87	3	1	11	32	...	2
88	...	...	9	29	3	9
89	...	...	14	16	10	18
90	1	2	17	7	26	28
91	1	...	5	2	32	51
92	1	...	4	3	51	37
93	1	1	...	...	58	25
94	...	...	...	...	49	16
95	...	...	...	...	27	5
96	...	2	...	...	14	6
97	...	...	...	2	2	...
98	3	1	...	...	2	1
99	1	...	1	...	...	1
100	2	...	2	...	1	1
101	2	...	...	3	1	...
102	...	...	1	...	...	...
103	...	...	2	1	1	4
104	...	...	5	2	1	3
105	...	...	4	...	2	1
106	....	...	3	...	3	1
107	...	...	3	...	6	2
108	...	...	2	...	8	2
109	...	...	...	...	6	...
110	...	...	...	...	6	...
111	...	...	...	...	7	...
112	...	...	...	...	5	1
113	...	...	...	...	1	...
Totals: 1 moult	26	35	79	135	277	204
Totals: 2 moults	12	6	23	8	48	16
Totals: combined	38	41	102	143	326[a]	220

[a] Includes 1 that did not moult.

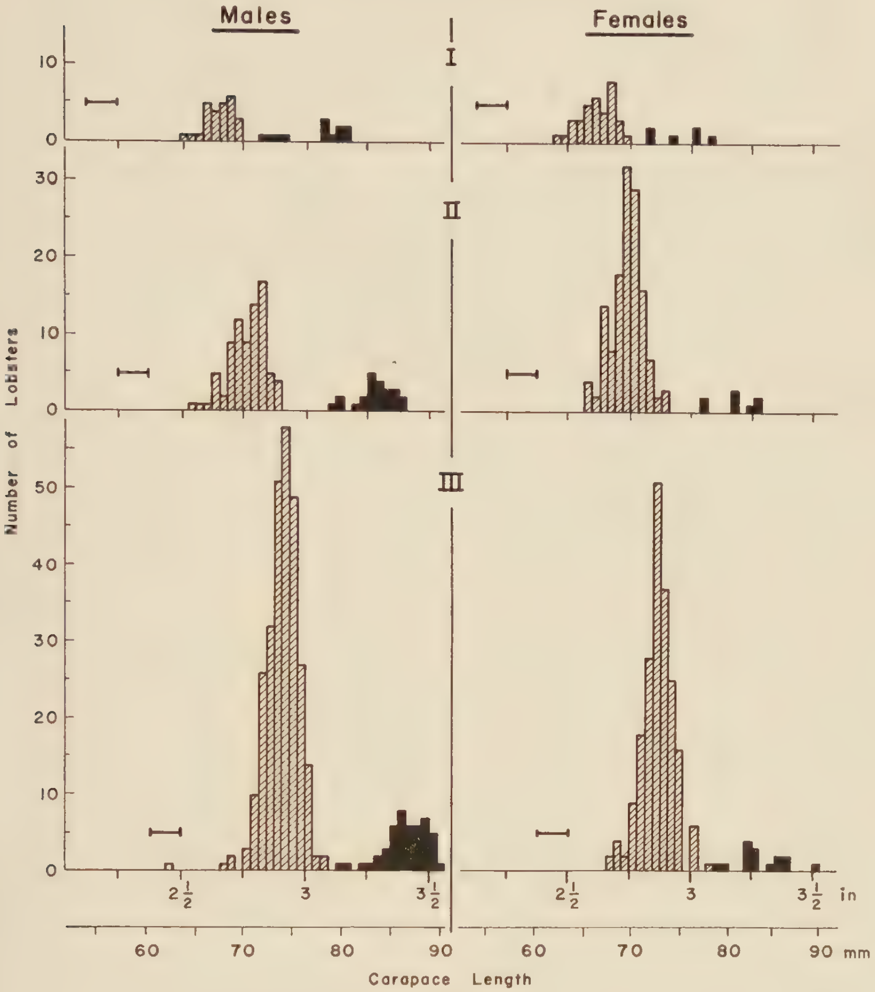

FIG. 4. Carapace-length distributions of 466 male and 404 female lobsters marked in three size-groups September 15 to October 4, 1954, and recovered August 4 to October 5, 1955. One moult — cross-hatched; two moults — black. ⊢⊣ indicates length range when marked.

involved. Group I size distributions suggest, however, that part of this group did not grow enough at the first moult to reach legal size ($2\frac{1}{2}$ in., 63.5 mm). These smaller lobsters being unexploited during the first half of the season would tend to reduce the average sizes attained at the second moult.

In Fig. 5 the post-moult carapace lengths are plotted against pre-moult carapace lengths for both the first and second moults. This method introduced by Hiatt (1948) has been applied to various species of crustacea by Kurata (1962). Straight lines of the form $Y = a + b X$ where Y and X are the post-

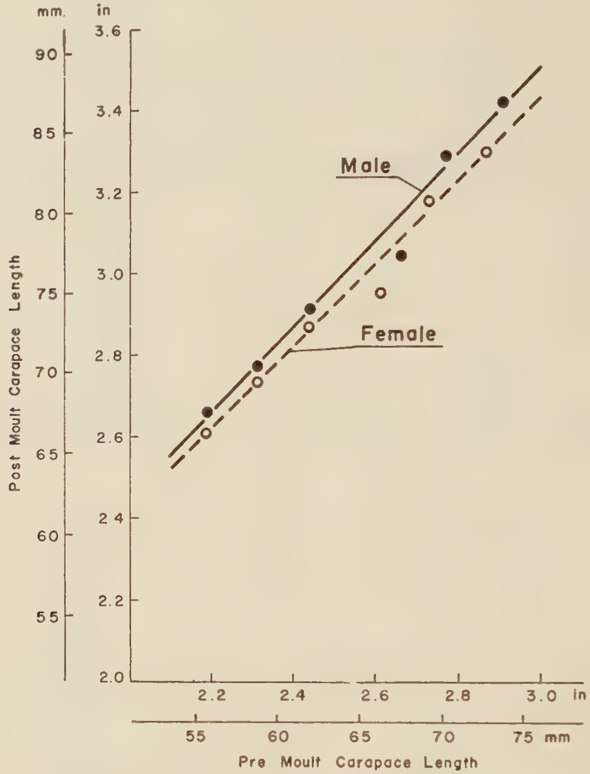

FIG. 5. Regression of post-moult length on pre-moult length for male and female marked lobsters.

TABLE III. Average carapace length and growth of marked lobsters in inches (1 inch = 2.54 cm).

		Group I		Group II		Group III	
Length when marked—mid-point:		2.19		2.31		2.44	
	Sex:	♂	♀	♂	♀	♂	♀
First moult	*n*	26	35	79	135	277	204
	$\bar{x}$	2.66	2.61	2.77	2.73	2.91	2.87
	Growth	0.47	0.42	0.46	0.42	0.47	0.43
	% growth	21.5	19.2	19.9	18.2	19.3	17.6
Second moult	*n*	12	6	23	8	48	16
	$\bar{x}$	3.04	2.95	3.28	3.17	3.41	3.29
	Growth	0.38	0.34	0.51	0.44	0.50	0.42
	% growth	14.3	13.0	18.4	16.1	17.2	14.6
Combined	*n*	38	41	102	143	326[a]	220
	$\bar{x}$	2.78	2.66	2.88	2.75	2.97	2.90
	Growth	0.59	0.47	0.57	0.44	0.53	0.46
	% growth	26.9	21.5	24.7	19.0	21.7	18.9

[a] Includes 1 that did not moult.

and pre-moult carapace lengths in inches have been fitted by least squares. The equations

$$Y = 0.344 + 1.051\,X \text{ for males}$$

and

$$Y = 0.414 + 1.004\,X \text{ for females}$$

fit the data well except for the Group I second-moult averages referred to above. With *b* values for both sexes approximating 1, the growth pattern for this phase (mainly juvenile) is of Kurata's type 3 (arithmetic growth) where successive growth increments are constant. The average increment per moult for males was 0.47 inches (11.9 mm) and for females 0.42 inches (10.7 mm). During the 10 to 12 months the lobsters were at liberty, the males on the average grew 0.55 inches (14.0 mm), the females, 0.45 inches (11.4 mm).

The average weights of lobsters marked and recovered are tabulated by sex and size-groups in Table IV. The weights were calculated from the author's carapace length-weight equation for Tignish, P.E.I. (Wilder, 1953). Average weights of lobsters recovered were calculated from average weights determined for each eighth-inch carapace length group. The growth per moult for males was 4.0–7.5 ounces (113–213 g), for females 3.3–5.4 ounces (94–153 g). In 10 to 12 months the males grew 5.5–6.1 ounces (156–173 g), the females 3.9–4.6 ounces (111–130 g).

TABLE IV. Average weight and growth of marked lobsters in ounces (1 ounce = 28.35 g).

		Group I		Group II		Group III	
	Sex:	♂	♀	♂	♀	♂	♀
	Average weight when marked:	4.6	4.9	5.5	5.8	6.5	6.7
First moult	*n*	26	35	79	135	277	204
	$\bar{x}$	8.6	8.2	9.9	9.5	11.5	10.9
	Growth	4.0	3.3	4.4	3.7	5.0	4.2
	% growth	87.0	67.3	80.0	63.8	76.9	62.7
Second moult	*n*	12	6	23	8	48	16
	$\bar{x}$	13.3	11.9	16.8	14.2	19.0	16.3
	Growth	4.7	3.7	6.9	4.7	7.5	5.4
	% growth	54.7	45.1	69.7	49.5	65.2	49.5
Combined	*n*	38	41	102	143	326[a]	220
	$\bar{x}$	10.1	8.8	11.4	9.7	12.6	11.3
	Growth	5.5	3.9	5.9	3.9	6.1	4.6
	% growth	119.6	79.6	107.3	67.2	93.8	68.7

[a] Includes 1 that did not moult.

SURVIVAL

Of the 6,716 marked lobsters released September 15 to October 4, 1954, a total of 870 were recovered during the 1955 season. The weights of lobsters examined and the number of marked found at the various ports where the search was conducted are listed in Table V.

At Abrams Village (including Cape Egmont) where four observers were stationed throughout the season it was possible to obtain a daily record of weight landed, weight examined and marked lobsters recovered. The data are summarized by weekly periods in Table VI. Weekly recoveries, adjusted according to the fraction of the catch examined, indicate that a total of 1,693 marked lobsters were recaptured there.

TABLE V. Weight (pounds) of lobsters examined and numbers of marked lobsters found at various ports in Prince Edward Island and New Brunswick during 1955 season (2.2 pounds = 1 kg).

Port	Weight examined	Marked lobsters found
	'000 lb	no.
Prince Edward Island		
Abrams Village	176.9	806
Mont Carmel	12.7	1
Summerside	29.9	0
Higgins Wharf	50.6	9
Brae Harbour	7.3	3
West Point	12.9	3
Cape Wolfe	5.3	0
Miminegash	9.3	0
Sub totals:	304.9	822
New Brunswick		
Cape Tormentine	17.6	0
Shemogue	6.8	0
Cape Bald	34.9	41
Cocagne	17.9	4
Richibucto	9.3	3
St. Louis	3.8	0
Pt. Sapin	9.9	0
Sub totals:	100.2	48
Totals:	405.1	870

TABLE VI. Weight (pounds) of "canner" (Can.) and market-sized (Mkt.) lobsters landed at Abrams Village each week during 1955 season. Weight examined, marked lobsters recovered and estimated number of marked caught at these ports (2.2 pounds = 1 kg).

	Weight landed		Weight examined		Marked lobsters			
					Recovered		Caught	
Week	Can.	Mkt.	Can.	Mkt.	Can.	Mkt.	Can.	Mkt.
	'000 lb		'000 lb		no.	no.	no.	no.
Aug. 10–16	134.6	33.7	48.3	1.0	319	0	890	0
" 17–23	36.7	13.4	26.8	2.7	238	1	326	5
" 24–30	20.6	7.6	15.8	1.9	96	1	126	4
" 31–Sept. 6	31.1	8.9	8.2	1.5	33	3	125	18
Sept. 7–13	38.4	9.5	18.8	5.1	14	22	29	41
" 14–20	40.4	9.2	16.3	4.7	4	25	10	48
" 21–27	20.4	4.5	9.6	2.1	1	17	2	36
" 28–Oct. 5	21.4	4.2	10.5	2.4	4	14	8	25
Totals:	343.6	91.0	154.3	21.4	709	83	1,516	177

Similar data for other ports in Prince Edward Island and New Brunswick are not complete enough to permit estimates of this type. A total recapture figure for all other ports combined can however be derived from the recovery of tags at these ports and the ratio of tagged to marked lobsters at Abrams Village. The ratio of tagged to untagged lobsters in the commercial landings at Abrams Village remained relatively constant during August. Thereafter the ratio fell rapidly, indicating further moulting that reduced the tagged stock through loss of tags and increased the untagged stock by recruitment to legal size. For this reason the following estimates are based on August data only:

Marked lobsters found at Abrams Village	670	
Estimated number of marked caught at Abrams Village	1,368	
1954 tags recovered at Abrams Village	109	
August ratio of tagged to marked 109:1,368	1:12.5	
1954 tags recovered in all other areas	100	
Estimated number of marked caught in all other areas (100 × 12.5)	1,250	
Estimated total recapture of marked during August	2,618	
1955 tags recovered—all areas	255	(51.0%)

$$\text{Estimated stock of marked lobsters on August 10, 1955} = \frac{2{,}618 \times 100}{51} \qquad 5{,}133$$

$$\text{Survival} = \frac{\text{Stock of marked lobsters on August 10, 1955}}{\text{Number released 1954}} = \frac{5{,}133}{6{,}716} = \qquad 76.4\%$$

This estimate of 76% survival over a 10-month period is, of course, subject to several errors. The tagged to marked ratio derived from Abrams Village data may not apply to the area as a whole. Distant tag returns are unlikely to be as complete as those from Abrams Village vicinity. The August rate of exploitation (51%) may not apply to the area as a whole. Of the 6,716 marked lobsters some may have been removed before or shortly after the close of the 1954 season. Further work is needed to establish reliable estimates of survival and natural mortality.

DISCUSSION

The Egmont Bay data on movements of tagged and marked lobsters confirm results of earlier studies that indicate limited movements. Extensive taggings at numerous ports within and around the fall-season area (Wilder, 1947) have failed to provide evidence of emigration or immigration. The high tag returns from the 1955 tagging (51% in 3 weeks) also confirm the conclusion reached earlier (Wilder, 1947) that throughout much of the fall-season area the rate of exploitation is extremely high. The rapid growth of lobsters released in 1954 indicates that the legal stock in any one year depends principally on recruitment rather than migration.

Under present conditions, spring stocks approximate the low levels that remain at the close of the intensive fall fishery. Fishing, particularly during early spring, would be considerably poorer since catchability is greatly reduced by cold water (McLeese and Wilder, 1958). That lobsters are actually present in spring, although greatly reduced in numbers by previous intensive fishing, has been amply demonstrated by the use of specially designed drags (Wilder, 1953; Anon, 1957).

All the available evidence indicates that the present fall-season area could, like other nearby areas, support a spring fishery if the lobsters were not removed the previous summer and early fall.

ACKNOWLEDGMENTS

R. C. Murray, who was in charge of field operations, tagged and marked the lobsters. He was ably assisted in the often tedious search for marked lobsters by D. W. McLeese, U. J. Walsh, W. A. Johnstone and Fisheries Wardens C. J. Yeo, B. S. Williams, A. W. Boyle and C. L. Heckbert. Without the enthusiastic co-operation and interest of many fishermen and lobster dealers, who willingly landed short lobsters and permitted examination of their catches often in warm weather, this study would not have been possible.

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The Movement of Tagged Great Slave Lake Fish[1]

By J. J. Keleher

Fisheries Research Board of Canada
Biological Station, London, Ont.

ABSTRACT

At Great Slave Lake, N.W.T., 3629 fish marked with Petersen tags were released during 5 years from 1946 to 1955. The time at large and movement of 505 recoveries, mostly lake whitefish, *Coregonus clupeaformis*, and lake trout, *Cristivomer namaycush*, are analyzed. Most of the tagged fish were caught in the summer commercial fishery; returns during the fall and winter were scarce. The median recapture time was 268 days; the maximum, for a lake trout, was 4027 days. Movement was generally limited; its median was 5 statute miles (8 km). A few fish travelled relatively long distances. There was no overall directional pattern to the movement, but some aggregation of the recaptured fish was noted. The fish populations are regarded as sedentary rather than mobile.

INTRODUCTION

Studies on the movement of fish in the larger lakes of North America have not been numerous. When carried out by marking individuals, some have utilized hatchery stock and others have employed spawning fish. The result is that the home range of the adult segment of the population is largely undefined, even though such information has applicability to taxonomic investigations, population estimates and fishery management. For this reason, a summary of a tagging study at Great Slave Lake is presented.[2] It involved the release, between 1946 and 1955, of 3629 fish bearing Petersen tags. Reports of recoveries totalled 505 fish and indicated a generally limited movement within the lake.

THE TAGGING PROGRAM

The majority of fish tagged were obtained from gill nets of 7 mesh sizes. No anaesthetic was used and the fish were liberated immediately afterwards. Table I shows the numbers of the 10 species tagged and subsequently recaptured. Usually not more than 10 individuals of a particular species were tagged each day. The total number of tagging days for lake whitefish, lake trout and longnose sucker was 114, 93 and 36, respectively. The fish were released generally where they were caught. To avoid innumerable release points, a general grouping consisting of 25 sites has been adopted. The site numbers follow a clockwise sequence commencing at Jones Point (Fig. 1).

Ninety-eight tagged fish were recaptured in the tagging gear. If viable, the fish was again liberated. This was termed a "re-release" and for enumeration purposes was counted as two tagged fish. There were 69 re-releases; two of them were caught again.

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[1] Received for publication September 5, 1962.

[2] Details are supplied in the Fisheries Research Board of Canada, Manuscript Report (Biology), No. 741, on file at all stations of the Board.

J. Fish. Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

TABLE I. Numbers of fish tagged and recaptured (in parentheses) at Great Slave Lake according to tagging years.

Scientific name	Common name	1946	1947	1953	1954	1955	Total
Coregonus clupeaformis	Lake whitefish	35 (9)	328 (35)	679 (62)	413 (45)	353 (53)	1,808 (206[a])
Cristivomer namaycush	Lake trout	77 (10)	504 (139)	228 (24)	22 (7)	171 (39)	1,002 (221)
Stenodus leucichthys	Inconnu	...	6 (2)	12 (1)	5 (1)	...	23 (4)
Esox lucius	Northern pike	...	...	42 (4)	37 (2)	59 (5)	138 (11)
Stizostedion v. vitreum	Walleye	...	...	56 (4)	19 (1)	7 (0)	82 (5)
Catostomus catostomus	Longnose sucker	...	...	284 (28)	44 (9)	3 (1)	331 (38)
Leucichthys spp.	Ciscoes	...	...	4 (0)	4 (0)	44 (2)	52 (2)
Lota lota	Burbot	...	...	42 (6)	62 (5)	8 (1)	112 (12)
Thymallus arcticus	Arctic grayling	...	...	1 (0)	32 (2)	2 (0)	35 (2)
Prosopium cylindraceum	Round whitefish	...	...	3 (0)	5 (0)	38 (2)	46 (2)
		112 (19)	838 (176)	1,351 (129)	643 (72)	685 (123)	3,629 (505[b])

[a] Includes 2 of unknown tagging year.
[b] Includes 2 unidentified species.

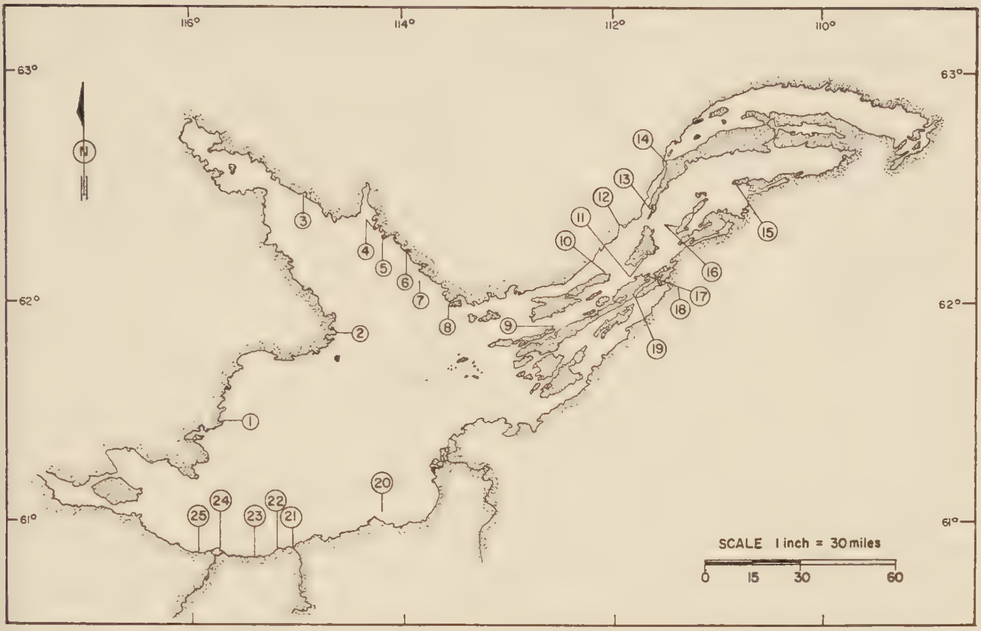

FIG. 1. General location of tagging sites at Great Slave Lake.

RECOVERIES OF TAGGED FISH

METHODS OF RECOVERY

Except for six individuals, all of the tagged fish were caught again in gill nets. Two ciscoes and one lake trout were eaten by lake trout. Anglers captured a lake trout, walleye and a burbot.

Most reports of recovered tags were made to this Board's field staff. Thirty-one reports were made to local Department of Fisheries of Canada personnel, and nine were received by other government departments. Personal contact with the fishermen was the main means of soliciting tag returns. No rewards were paid, but usually the tagging information was supplied verbally or by letter.

Board personnel made 100 recaptures; 13 were caught by Treaty Indians and others; the remainder (378 positively and 14 presumably) were caught by commercial fishermen.

RECAPTURE RATE OF RECOVERIES

The recapture percentages for each species can be derived from Table I. For some species it was influenced by Board recaptures. By excluding these, the lake trout percentage decreases to 18; the lake whitefish and inconnu decrease to 9. Board recaptures for the others were: northern pike and Arctic grayling, 1; round whitefish, 2; longnose sucker, 3.

By comparing the number of summer commercial fishermen reporting tagged fish with the total number, it was concluded that unreported recaptures in the summer commercial fishery were infrequent. Probably a greater propor-

TABLE II. Number of fish recovered in relation to calendar year tagged.

	Calendar year after tagging								
	0	1	2	3	4	5	6	7	Total
Lake whitefish	95	69	25	7	2	5	...	1	204
Lake trout	97	55	34	11	8	5	2	...	219[a]
Inconnu	3	...	1	...	...	...	...	...	4
Northern pike	4	3	...	4	...	...	...	...	11
Walleye	1	3	...	...	1	...	...	...	5
Longnose sucker	15	11	5	3	1	2	...	1	38
Ciscoes	1	...	...	1	...	...	...	...	2
Burbot	1	6	2	2	1	...	...	...	12
Arctic grayling	2	...	...	...	...	...	...	...	2
Round whitefish	2	...	...	...	...	...	...	...	2
Total:	221	147	67	28	13	12	2	2	499

[a] Includes 2 at 8, 4 at 9, and 1 at 11 years.

tion of unreported tags occurred in the fall domestic and winter commercial fisheries. The ratio of summer to winter tag returns was 7 to 1. The winter fishery was not conducted generally near all the tagging sites, and the tagged fish possibly were less available in the winter. Seasonal recapture differences resulted therefore from differential opportunities for catching and reporting the tagged fish.

TIME OF RECOVERIES

The period that the fish were at large was calculated both by reference to the number of calendar years after tagging and the actual days. These data are aberrant because the fish were not equally vulnerable to recapture throughout the year. One feature of Table II is the long interval before recapture for some fish. The record was a lake trout tagged 4027 days previously (11 + years) at site 15. It was caught one mile (1.6 km) away on August 26, 1958. Six lake trout were caught from 8 to 9 years later. A lake whitefish and longnose sucker were caught in the 7th year. Twenty-six percent of all recaptured fish were taken subsequent to the first calendar year after tagging.

Figures on a daily basis are presented in Table III. Five species (lake trout, northern pike, walleye, longnose sucker and burbot) were at liberty for similar periods. Their means are between 455 and 581 days, the medians between 260 and 347 days. Lake whitefish had a shorter period—mean and median of 296 and 159 days. The recapture intervals for lake whitefish and lake trout are depressed by the Board recaptures. In any case, the limited number of returns prevents any intensive analysis.

MOVEMENT OF RECOVERIES

Movement was expressed in two ways—first by distance alone and secondly by direction, dependent on distance. The shortest line between release and recapture was regarded as the fish's movement. It was measured in whole

TABLE III. Statistics for days at large of Great Slave Lake recaptured tagged fish.

	No.	Total	Mean	Median	Maximum
Lake whitefish	199	58,872	296	159	2,457
Lake trout	213	100,392	471	327	4,027
Inconnu	4	691	173	1	684
Northern pike	11	5,476	498	340	1,116
Walleye	5	2,276	455	260	1,425
Longnose sucker	36	18,131	504	283	2,736
Cisco	1	1,052	...	...	1,052
Burbot	12	6,969	581	347	1,433
Arctic grayling	2	10	5	...	7
Round whitefish	2	3	2	...	2
All species	485	193,872	400	268	4,027

statute miles on 1:250,000 hydrographic charts. The direction was expressed as a true azimuth. Component miles for each recaptured fish, used in computing the average net movement from each site, were calculated by trigonometric formulae.

Distances between release and recapture usually were small (Table IV). Fifty percent were within 5 miles (8 km), and 64% were within 10 miles (16 km). This generally limited movement is emphasized by the relatively long mean recapture time of 400 days. Some fish, however, travelled considerable distances; six moved in excess of 100 miles (160 km) each. Table IV refers only to movement within the lake. Three fish were found in contiguous rivers.

On October 23, 1953, a lake whitefish was released at site 25. This fish probably was a "non-spawner" (*see* Kennedy, 1953). It was recaptured on September 14, 1954 in a net near Fort Simpson, N.W.T. The movement was 239 miles (382 km), 215 miles (344 km) of which were in the Mackenzie River. The other two fish moved up the Slave River from site 24. A walleye was caught on June 1, 1954 by angling "near the mouth of the Salt River". In 260 days it moved 236 miles (378 km), 163 (261) in the river. A burbot was recaptured at Fort Smith 90 days after its release on September 19, 1953. Its movement was computed as 254 miles (406 km), the lake portion being 73 (117).

Fish recaptured soon after release had hardly moved; 15 miles (24 km) was the maximum for lake whitefish or lake trout recaptured within 14 days. Nevertheless, considering the entire range of observations, movement was not correlated with days at large. The distance travelled by lake whitefish was influenced by the time of release. Releases in October had a median of 24 miles (38 km), as opposed to medians of 5 and 9 miles (8 and 14 km) for September and June. This was not evident in the other species. Some regional differences also were noted. Lake whitefish and lake trout released in the East Arm (sites 9–19) showed little movement; lake whitefish from the North Arm (sites 3–7) showed twice the movement observed overall; lake trout released from site 2 were exceptionally mobile.

TABLE IV. Movement within Great Slave Lake.

No. of miles	Lake whitefish	Lake trout	Northern pike	Longnose sucker	Burbot	Total
?	7	7	...	3	...	20[a]
0	48	51	1	3	1	109[b]
1	27	42	1	...	1	72[c]
2	6	5	...	1	1	16[d]
3	7	6	1	3	...	17
4	8	2	...	2	2	15[e]
5	4	9	1	1	1	16
6	7	6	...	...	...	13
7	4	4	2	2	1	13
8	5	5	...	2	...	13[e]
9	6	6	...	1	1	14
10–19	31	26	3	8	1	69
20–29	18	11	1	3	1	35[c]
30–39	10	16	1	6	...	33
40–49	8	9	...	3	...	20
50–59	6	7	...	...	...	13
60–99	1	6	...	...	2	11[f]
100–209	3	3	...	...	...	6

[a] Includes 1 cisco and 2 unidentified.
[b] Includes 2 inconnu, 1 grayling and 2 round whitefish.
[c] Includes 1 inconnu.
[d] Includes 1 walleye, 1 cisco, 1 grayling.
[e] Includes 1 walleye.
[f] Includes 2 walleye.

The speed of movement was calculated in terms of miles per day. The average rate was highest for longnose sucker with 0.3 mile (0.5 km) per day. Ten lake whitefish, 7 lake trout, 5 longnose sucker and 1 burbot exceeded 0.9 mile (1.4 km) per day. The best daily speed over a sizeable distance and time was 4.5 miles (7.2 km). This lake whitefish, released at site 13, moved 122 miles (195 km) to the North Arm, being captured 27 days later. Another notable rate was that for the burbot recaptured at Fort Smith.

In order to ascertain any definite directional aspect to the movement of two species, the average net movement from the sites was computed (Table V). As an example: at site 1 the average net components for lake trout movement were 11.5 miles (18.5 km) south and 7.4 miles (12 km) east. Thus the average movement of recaptured lake trout from site 1 was 13.7 miles (22 km) on an azimuth of 123°. The obvious feature to the directional pattern is its variety. When the azimuths are applied at the site locations, no more meaningful pattern emerges. The preponderance of values along the east-west axis corresponds to the position of the lake's basin.

Although movement was diverse enough so that no overall directional basis was evident, some tagged fish were caught together. The best examples are presented in Table VI. It shows 9 cases where fish, usually released together, were recaptured together. The first 4 cases involve little movement over a long

TABLE V. Average net movement for recaptured lake whitefish (L.W.) and lake trout (L.T.). Data for less than five recaptures per site are omitted.

Species	Site No.	No. of fish	Mean difference (component miles)		Mean net	
			N. & S.	E. & W.	Miles	Azimuth (degrees)
L.W.	3	15	12.8	2.0	12.9	189
	5	6	2.5	0.4	2.5	189
	8	17	0.2	3.3	3.3	149
	9	25	0.4	1.6	1.6	284
	11	21	0.8	0.2	0.8	194
	12	6	1.0	1.3	1.6	232
	13	25	0.8	3.2	3.3	256
	17	19	1.0	2.0	2.2	243
	20	8	0.9	2.0	2.2	246
	22	28	12.4	2.4	12.6	349
	24	10	6.1	2.6	6.6	337
	25	13	34.6	16.5	38.3	25
L.T.	1	10	11.5	7.4	13.7	123
	2	12	13.8	8.3	16.1	211
	8	13	0.8	1.9	2.1	67
	10	5	0.3	2.9	2.9	132
	11	41	0.7	4.2	4.3	261
	12	27	4.9	9.7	10.8	243
	13	8	3.7	7.7	8.5	64
	15	46	11.0	16.8	20.1	237
	16	7	0.3	7.5	7.5	272
	17	7	0.4	1.2	1.3	288
	25	18	2.8	1.8	3.3	33

period, while the others represent movement over relatively considerable distances. Some tagged fish therefore tended to remain together whether they were sedentary or mobile.

SUMMARY AND DISCUSSION

Fourteen percent of Great Slave Lake fish tagged over a 10-year period at a variety of locations were reported recovered. Lake whitefish and lake trout were tagged and recovered in the greatest numbers. Longnose sucker and seven other species were tagged and recovered in lesser numbers. The majority of tagged fish were caught in the calendar years following tagging. Nearly two-thirds were recovered within 10 miles (16 km) of their release. A few fish travelled considerable distances, both within the lake and in drainage rivers. Although some aggregation among tagged fish was found, an absence of any overall directional pattern to the movement was exhibited.

The observed movement of the recaptured fish over relatively long periods indicates sedentary rather than mobile populations. This conclusion is rein-

TABLE VI. Examples of aggregation of recaptured tagged fish.

No.	Species	Days out	Miles moved	Azimuth	Date		Site No.
					Tagged	Recaptured	
1	Lake trout	1821	1	1	Aug. 14, 1947	Aug. 10, 1952	15
2	Lake trout	733	0	0	Sept. 7, 1947	Sept. 10, 1949	8
3	Lake whitefish	722	4	115	July 20, 1954	July 12, 1956	20
	" "	723	2	115	July 21, 1954	July 14, 1956	20
4	Lake trout	731	9	45	Sept. 4, 1947	Sept. 5, 1949	12
	" "	730	9	45	Sept. 5, 1947	Sept. 5, 1949	12
5	Lake whitefish	342	30	27	July 31, 1955	July 8, 1956	13
	" "	340	30	27	Aug. 2, 1955	July 8, 1956	13
6	Lake trout	344	37	246	Sept. 5, 1947	Aug. 15, 1948	12
	" "	345	37	246	Sept. 6, 1947	Aug. 17, 1948	12
7	Lake trout	681	36	179	Aug. 26, 1947	July 8, 1949	1
	" "	678	41	164	Aug. 27, 1947	July 6, 1949	1
8	Lake trout	710	34	236	Aug. 28, 1947	Aug. 8, 1949	2
	" "	718	34	236	Aug. 28, 1947	Aug. 16, 1949	2
9	Lake whitefish	605	33	295	Oct. 19, 1953	June 16, 1955	22
	" "	609	37	295	Oct. 19, 1953	June 20, 1955	22

forced when the size of their habitat is considered. Great Slave Lake fish thus conform to the habits of many other fish populations (*see* Gerking, 1959).

Indirectly, movement in Great Slave Lake fish populations has been indicated previously. On the basis of a regional difference in size of lake trout, Rawson (1951) postulated that there "is a general migration to the west during the life of these fish". Kennedy (1953) suggested that immigration of lake whitefish into the East Arm was responsible for the age structure of the population there. The results of the present study do not support these conclusions.

ACKNOWLEDGMENTS

All personnel involved in the Board's investigation at Great Slave Lake since 1946, many commercial fishermen, and others have contributed to this tagging study. It is a pleasure to record their help. I must mention particularly Drs W. A. Kennedy and D. C. Scott, who did the tagging in 1946–47 and 1953–55 respectively, and Mrs Marlene Kennings, whose painstaking work provided the source documents for the analysis of the data.

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Influence of Pond Formation on Brook Trout Movements and Angling Success[1]

By M. W. Smith

Fisheries Research Board of Canada
Biological Station, St. Andrews, N. B.

ABSTRACT

A 13-acre pond was formed at head of tide on Wilmot Stream, Prince Edward Island, to hold brook trout (*Salvelinus fontinalis*) moving between stream and saltwater estuary for greater availability to anglers. Trout continued to move between pond and estuary via an artificial outlet, predominantly during the spring and early summer. Improved angling conditions resulted in capture of 8,215 trout from pond and upper reaches of estuary at rate of 1.2 per rod-hour over three angling seasons. Shallowness of water limited trout-holding capacity of the pond and curtailed better angling success. Other hydrographic conditions and food supply in the pond were favourable for brook trout.

INTRODUCTION

Ponds formed on the spring-fed streams of Prince Edward Island are favourable habitats for brook trout, *Salvelinus fontinalis* (Mitchill). The ponds are readily accessible to anglers, and fishing success is generally good (Smith, 1951).

Brook trout move between fresh and salt water in the Prince Edward Island area, as well as elsewhere in the Maritime Provinces of Canada (Smith and Saunders, 1958; White, 1940). Height of dams holding Prince Edward Island ponds is almost invariably sufficient to stop upstream movements of trout. However, a number of fishing ponds have been established by the Prince Edward Island Department of Industry and Natural Resources with provision for inward and outward movements by trout. The ponds — called by-pass ponds — are formed by constructing re-enforced earthern embankments across stream valleys at sites suitable to create ponds, then providing artificial outlets around one end of the embankments. The outlets are usually sufficiently large to take care of flood waters without flow over the embankments.

Results of a study at a by-pass pond on the lower reaches of Wilmot Stream, Prince Edward Island, during the open-water season of three years, 1956–58, are herein reported. Primary objectives were to determine the extent and time of trout runs into and out of the pond through the artificial pond outlet, to assess angling success in the pond and contiguous stream areas, and to evaluate how well the pond served as holding area for upstream-moving trout as might be judged from anglers' catches.

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[1] Received for publication August 3, 1962.

. Fish. Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

STREAM AND POND

STREAM

Wilmot Stream drains approximately 70 sq mi (1 sq mi = 2.590 sq km) of farm land. Headwaters are at an altitude of about 200 ft (1 ft = 0.3038 m), and the stream flows westerly, close to 46°25′N latitude, into Bedeque Bay, an inlet from Northumberland Strait on the south coast of Prince Edward Island. The long axis of the watershed is about 12 mi (1 mi = 1.609 km). The stream is tidal from the pond embankment downstream to Bedeque Bay, a distance of about 4 mi.

POND

MORPHOMETRY. The pond was formed in 1951 on an old mill-pond site. The area of the pond, as determined from a survey made over ice, is 13.0 acres (1 acre = 0.4047 ha) (Fig. 1). Arbitrarily the boundary between pond and tributary stream is placed where the depth of water in the flooded stream bed falls below 5 ft at summer levels. The pond is shallow with an average depth of 3½ ft. In the flooded stream bed, which makes up 20% of the pond area, water depths vary from 5 to 9 ft except in a small area immediately above the embankment where a maximum depth of 12 ft is found.

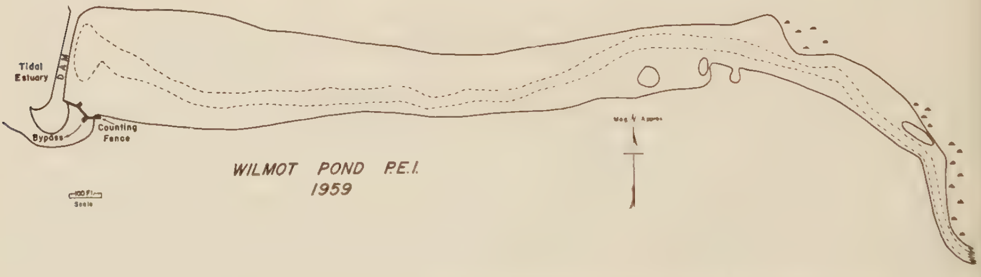

FIG. 1. Map of Wilmot Pond. Flooded stream area indicated by broken lines.

HYDROGRAPHY. Surface water temperature was recorded daily between 8 and 10 a.m. at the lower end of the pond during the periods of investigation. Mean temperatures for 2-week intervals during 1956–58 are plotted in Fig. 2. The highest recorded surface temperature was 18.8°C on August 7, 1956. At that time the temperature at 3 ft was 12.4° and at the bottom (12 ft) 12.1°C. Afternoon temperatures were doubtless higher, but we may safely conclude that the pond presents a favourable cool habitat for brook trout throughout the summer.

The dissolved oxygen content of the water was determined on a number of occasions. On any one date, samples were obtained from the surface and bottom at three stations, one each in the lower, central and upper parts of the pond. The range in values is given in Table I. The water was found invariably supersaturated with oxygen during the summer months (day-time). Lower oxygen values were encountered in the autumn, but they showed only minor deficiencies. Flow of water through the pond then, and during the ice-covered

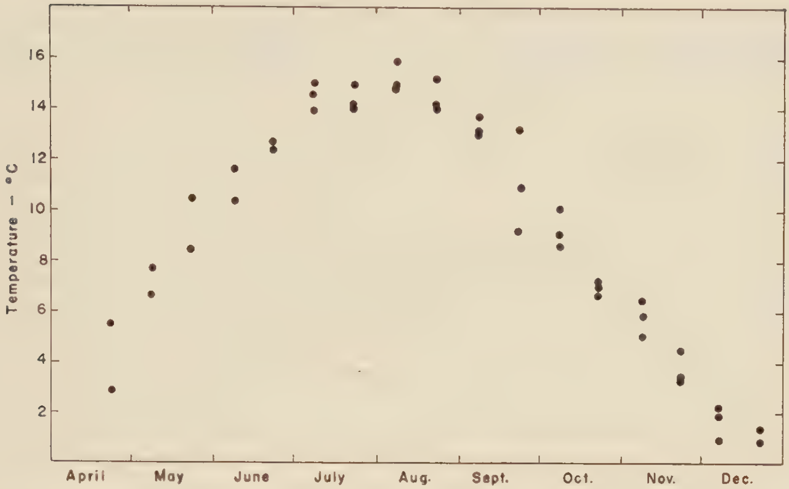

FIG. 2. Morning surface water temperature of Wilmot Pond. Bi-monthly means, 1956–58.

TABLE I. Range in dissolved oxygen content and pH values of water in Wilmot Pond.

Date	Dissolved oxygen ml/l	Dissolved oxygen Saturation	pH
1956		%	
Aug. 7	9.4–10.1	124–166	8.5–9.2
Sept. 25	8.9– 9.8	108–119	8.2–8.6
1957			
June 10	9.3– 9.8	121–128	8.5–8.8
July 8	8.6–10.6	117–160	8.2–9.0
July 19	9.3–10.7	122–151	8.4–8.9
Aug. 12	7.7– 8.6	105–127	8.0–8.6
Oct. 10	7.9– 8.3	101–109	7.9–8.0
1958			
June 18	9.2–10.0	123–136	8.4–8.8
Sept. 18	7.4– 9.7	92–123	7.8–8.4
Oct. 17	7.2 - 8.3	88–100	7.9

period, would appear adequate to obviate any serious reduction in oxygen content during the cold-water season.

The water of the pond was alkaline. Determined values of pH ranged from 7.8 to 9.2 (Table I).

MACROBENTHOS. Bottom organisms were sampled on eleven occasions during 1956–58 with a Petersen dredge (117 sq inches) (1 sq inch = 6.451 sq cm). Sampling on the several dates consisted of a single grab at each of 17 stations, 6 in the old stream bed and the remainder scattered over the flooded areas. While still alive, the organisms were sorted from the bottom materials by washing through a set of sieves of which the finest had a mesh size of 1 mm. The average number of organisms per square metre for the several sampling dates are given in Table II.

Aquatic earthworms (oligochaetes) and midge larvae (chironomids) dominated the bottom fauna numerically. Loftus (1948) found a similar situation in three other artificial ponds formed on Prince Edward Island streams. He noted that aquatic earthworms were rarely eaten by brook trout, possibly because these forms were not available as food. In the case of Wilmot Pond, even if we discount the aquatic earthworms as food items, it appears, however, that the other organisms, most of which are known to be eaten by brook trout, provided good forage.

TABLE II. Wilmot Pond bottom fauna. Average numbers per square metre.

Date	Stations	Aquatic earthworms	Leeches	Amphipods	Midge larvae	Misc. larval insects	Snails	Sphaeriids
1956								
Aug. 20	a*	93	0	4	232	0	40	11
–21	b	86	0	0	181	28	1	28
Nov. 7	a	0	2	0	119	0	0	4
–8	b	75	1	1	234	9	0	75
1957								
June 12	a	29	0	0	174	13	7	4
–13	b	335	0	0	49	5	1	20
Aug. 12	a	35	0	0	318	7	0	0
–14	b	2471	0	93	449	65	1	29
Sept. 17	a	31	0	2	781	7	4	2
–19	b	532	0	0	251	20	3	82
Oct. 16	a	24	0	0	86	2	0	0
–17	b	70	0	0	278	0	0	4
1958								
July 10	a	4	0	0	84	4	0	13
–11	b	528	1	0	9	8	1	8
Aug. 11	a	13	0	0	22	0	0	0
–12	b	149	1	0	278	50	4	107
Sept. 8	a	49	0	0	0	0	0	0
– 9	b	173	1	0	241	131	0	78
Oct. 16	a	11	0	0	4	0	0	0
–17	b	94	0	2	267	17	7	127

*a—6 stations in old stream bed; b–11 stations in flooded area.

POND OUTLET

The length of the pond outlet is 300 ft in which distance the water falls 9½ ft. The gradient is not uniform, however, being greatest in the lower half of the outlet. In this lower section, in a distance of 20 ft there are almost vertical falls of 12, 14 and 24 in (1 in = 2.54 cm). As data to be given later illustrate, these falls were readily negotiated by upstream-moving trout.

Minimal discharge of water from the pond through the outlet approximated 30 cu ft/sec (1 cu ft = 0.02832 cu m), and was observed during November 1956 and again in late September and early October 1957.

MOVEMENTS OF TROUT INTO AND OUT OF WILMOT POND

Method of Study

Trout moving into and out of Wilmot Pond were captured in traps incorporated in a barrier constructed across the head of the pond outlet. Design and construction of the barrier and traps were similar to those described by Smith and Saunders (1956).

The barrier and traps were not maintained throughout the winter. Periods of operation were June 14, 1956, to January 3, 1957; April 17, 1957, to January 15, 1958; April 5 to December 12, 1958.

Table III. Number of brook trout tagged as they moved upstream into Wilmot Pond, and records of subsequent recapture.

Year and month	Number tagged	Not recaptured	Angled in pond	Angled in stream above pond	Returned downstream	Angled in estuary	Second movement upstream
1956							
June	1552	1148	237	66	104	10	22
July	577	426	73	15	65	7	7
Aug.	10	7	1	0	2	0	0
Sept.	29	22	1	0	6	1	0
Oct.	166	115	23	2	30	7	9
Nov.	127	84	15	0	29	12	9
Dec.	5	2	3	0	2	0	1
1957							
Jan.	0	0	0	0	0	0	0
Apr.	0	0	0	0	0	0	0
May	6	3	1	0	2	1	0
June	1132	778	155	54	148	33	42
July	372	267	29	14	62	15	12
Aug.	8	6	1	0	1	0	0
Sept.	38	11	3	0	24	6	2
Oct.	61	26	1	0	32	10	4
Nov.	119	67	9	1	43	19	5
Dec.	5	5	0	0	0	0	0
1958							
Jan.	2	2	0	0	0	0	0
Apr.	4	2	2	0	0	0	0
May	17	12	5	0	0	0	0
June	899	787	66	42	4	0	1
July	393	336	29	22	6	0	2
Aug.	20	18	0	1	1	0	0
Sept.	11	10	0	1	0	0	0

The traps were tended daily. Captured trout were enumerated, measured (fork length) and tagged with a numbered, monel-metal jaw-tag (Smith and Saunders, 1958). The adipose fin was also removed so that trout which lost tags could be recognized when recaptured. Trout so recognized during the course of the investigation numbered 149.

Number of Trout

The numbers of trout tagged as they moved into and out of the pond are given by months in Tables III and IV. Total numbers tagged going upstream were 2,466 in 1956, 1,741 in 1957 and 1,346 in 1958. The numbers tagged going downstream in the same years were 303, 1,007 and 1,268, respectively. Tagging ceased on September 30, 1958. Some tagged trout made return movements through the traps. Accordingly, the numbers of movements by trout through the traps were higher, 6,287 in total upstream and 3,044 in total downstream, for the 3 years of operation.

TABLE IV. Number of brook trout tagged as they moved downstream out of Wilmot Pond, and records of subsequent recaptures.

Year and month	Number tagged	Not recaptured	Angled in estuary	Returned upstream	Angled in pond	Angled in stream above pond	Second movement downstream
1956							
June	37	21	4	12	2	1	2
July	2	2	0	0	0	0	0
Aug.	0	0	0	0	0	0	0
Sept.	13	8	1	3	1	0	1
Oct.	58	42	3	9	2	0	0
Nov.	124	86	10	20	5	1	1
Dec.	69	49	3	8	1	0	2
1957							
Jan.	6	5	0	1	0	0	0
Apr.	71	38	15	18	6	0	1
May	564	255	109	203	28	13	11
June	11	7	2	3	0	1	1
July	0	0	0	0	0	0	0
Aug.	5	4	0	1	0	0	0
Sept.	14	10	3	1	0	0	0
Oct.	17	12	3	2	1	0	0
Nov.	243	143	37	63	13	1	2
Dec.	76	49	13	13	3	0	1
1958							
Jan.	36	23	5	8	0	0	0
Apr.	841	483	177	180	29	10	3
May	387	213	78	94	15	5	1
June	1	1	0	0	0	0	0
July	1	1	0	0	0	0	0
Aug.	0	0	0	0	0	0	0
Sept.	2	2	0	0	0	0	0

TIME OF MOVEMENTS

As illustrated in Fig. 3, dominant downstream movements were encountered in April and May, and upstream in June and July. Few trout moved in mid summer. With less trout involved than in the early season runs, both downstream and upstream movements occurred during the fall and early winter. During this season trout moved both upstream and downstream on the same day in contrast to the situation in spring and early summer when the upstream and downstream movements were quite separated in time. The traps were maintained until January 15 in 1958. In the period January 1–15 of that year, 64 trout moved into the pond and 4 downstream. However most of these fish moved early in the month, and it appears probable that few trout moved into or out of the pond when winter conditions prevailed.

The movements of trout noted above at Wilmot Pond were quite comparable in time with movements between fresh and salt water observed previously at Ellerslie Brook, Prince Edward Island, when this stream was unobstructed by a dam (Smith and Saunders, 1958). However, a notable dissimilarity was the strong upstream movements at Ellerslie Brook in April, not recorded at Wilmot Pond. The upstream movements into Ellerslie Brook occurred when the temperature of the water in the stream went above 2°C. The traps were in operation at Wilmot Pond on April 17 in 1957 and on April 5 in 1958. It appears improbable that any appreciable April upstream movements at Wilmot were missed in view of the water temperatures that obtained and the almost complete absence of trout that might have indicated the tail-end of earlier upstream runs (Fig. 3). However, the possibility of an early spring run cannot be entirely ruled out.

The trout mostly moved into the traps at night, especially during early hours of darkness.

SIZE AND AGE OF TROUT

Length frequencies among the trout when tagged moving upstream and downstream are shown in Fig. 4. The age of 305 trout taken by anglers between July 30 and September 15, 1956, was determined by scale reading. The mean fork length with its standard deviation was 14.8±2.08 cm (n = 176) for age I, 17.3±2.15 cm (n = 108) for age II, and 22.4±2.45 cm (n = 20) for age III (1 cm = 0.394 inch). One trout, 30.3 cm in length, was age IV or V. The observed mean length at age I may be biased upward by the possibility that anglers took and retained the larger individuals in this age group. In any event, it is apparent from Fig. 4 that the trout moving into and out of Wilmot Pond were mostly young fish, preponderantly age I and II.

RECAPTURE OF TAGGED TROUT

Tagged trout were recaptured when they again moved into or out of the pond. Recaptures were also made by anglers. The record for recaptures of tagged trout is given in Tables III and IV.

Of the 8,131 trout tagged as they moved into and out of the pond, 1,200 (15%) were subsequently recaptured in the traps once, 142 (2%) twice, 14 three

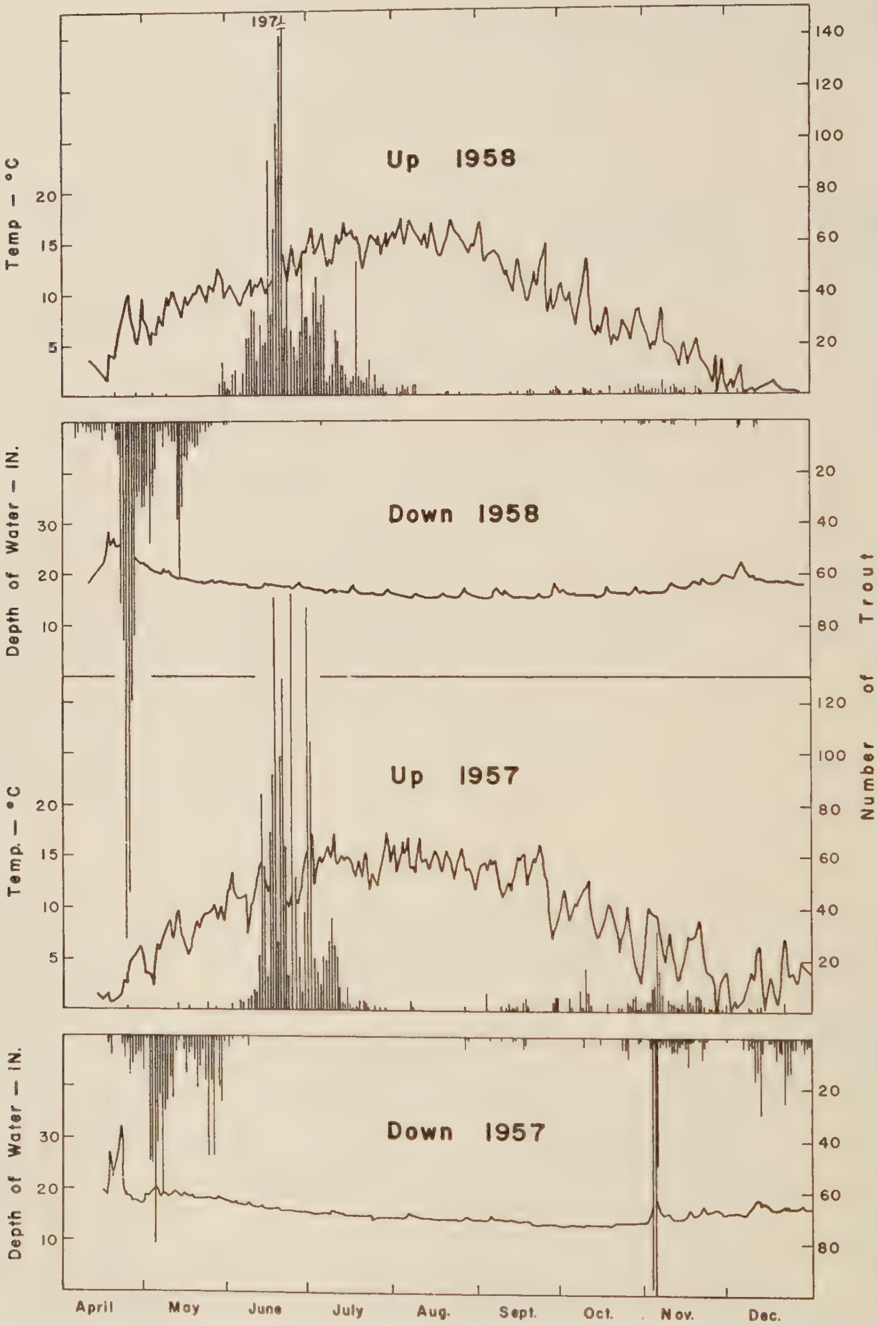

FIG. 3. Number and season of brook trout movements into and out of Wilmot Pond, with water temperature and change of water level of pond.

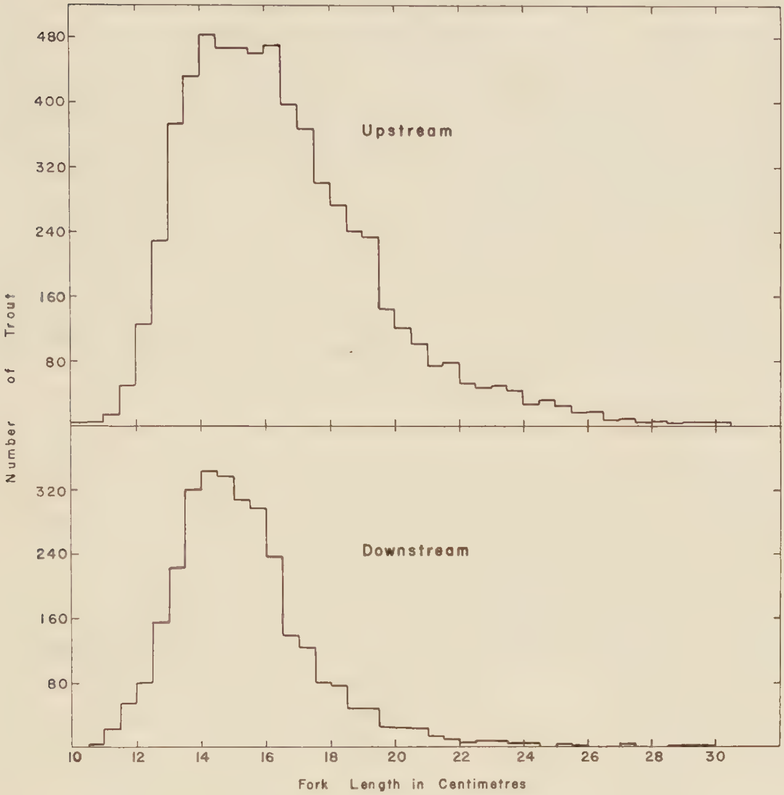

FIG. 4. Length frequencies among the brook trout that moved into and out of Wilmot Pond, 1956–58.

times and 2 four times. Anglers captured 1,594 (20%). For the majority of the tagged trout (5,588; 69%), there are no records of recapture. Some of the trout tagged moving either upstream or downstream in 1956 and 1957 were recaptured in next year by angling or in the traps. However, for those tagged in 1956 there are no records for recapture in 1958. These observations, corroborated by the length and age frequencies shown in Fig. 4, indicate that the brook trout in the Wilmot Stream system are short-lived, with few reaching age IV.

MOVEMENTS IN RELATION TO WATER CONDITIONS

Trout moved into and out of Wilmot Pond, that is between fresh and salt water, with rising temperature of water in spring and early summer, and again with falling temperature in the fall (Fig. 3). Movement almost entirely ceased in mid summer and, so far as we can judge, in mid winter and early spring as well. This pattern of movements is in general agreement with what was observed by Smith and Saunders (1958) for movements of trout between fresh and salt water at Ellerslie Brook, Prince Edward Island.

Experimentally it has been shown that with rising temperature, brook trout acclimated to a given temperature select a somewhat higher level until the range of 14–18°C is reached, when acclimation and selected temperatures coincide (Fry, 1951). Trout acclimated to temperature above 18°C, yet still sub-lethal, select somewhat cooler water. These relationships were advanced by Smith and Saunders (1958) to explain in part at least the cessation of movements into and out of Ellerslie Brook in midsummer, and would appear equally applicable in explanation of the similar observation at Wilmot (Fig. 3). Cessation of movements in winter could result from inactivity by trout at temperatures near 0°C.

At Ellerslie Brook movements of trout were closely associated with changing water level of the stream. "For most movements it appeared that temperature conditioned the trout to move and change in current provided the stimulus" (Smith and Saunders, 1958). This statement would also appear to hold with respect to the downstream movements in April and May, and to those both up and down in the autumn and early winter at Wilmot Pond (Fig. 3). At the time of the June–July upstream runs, particularly during those in 1957, the pond level progressively fell, however, with concurrent decline in the volume of water being discharged from the pond by the artificial outlet. Notwithstanding this situation, trout in the estuary near the effluence of the pond outlet would encounter a marked change in flow and turbulence of water over what would be experienced in the estuary. These conditions, although the outflow was gradually diminishing, may well have provided sufficient variation in current of water necessary to stimulate upstream movements of trout present in the area, simulating in effect spates in an unobstructed brook and agreeing with results obtained by Elson (1940) under experimental conditions.

YIELD OF TROUT TO ANGLERS

CREEL CENSUS

The angling season in 1956 and 1957 was from April 15 to September 15 inclusive. In 1958 the season was extended to September 30.

A creel census was conducted at Wilmot Pond and Estuary during the angling seasons 1956 to 1958, except that it was not begun in 1956 until May 3. Most of the angling in the estuary was within 500 yd (1 yd = 0.9144 m) of the pond embankment. The creel census taker was resident at the pond, and the census approached completeness for the pond and estuary. Angling in the pond was almost entirely from boats, while that in the estuary was completely from shore. Census data from each angler by personal contact included number of trout caught, time spent in fishing, where and how fishing was done, and length measurements of the fish.

Trout were also captured from the stream above the pond. An attempt was made to obtain records of tagged trout taken in this area. Knowledge that much of the angling was done along favoured stretches of the stream was helpful, but the record was incomplete.

NUMBER OF TROUT AND RATES OF CAPTURE

The recorded catch from the pond for the three angling seasons was 5,330 trout, taken at rates of 0.9 per rod-hour and 2.3 per rod (Table V). Less effort was expended on the estuary where 2,885 trout were taken at somewhat higher rates of 1.3 per rod-hour and 2.5 per rod or fishing trip (Table VI). Consolidated census records for the pond and estuary show that anglers took 8,215 trout at rates of 1.2 per rod-hour and 2.3 per rod. The above rates of capture are below those, 1.4 to 2.5 per rod-hour, observed for Montague Pond, Prince Edward Island, over a ten-year period (Smith, 1954). However, they are above rates, 0.2–0.8 per rod-hour, determined for a number of soft-water New Brunswick and Nova Scotia lakes (Smith, 1948, 1952).

In addition to the above catches from pond and estuary, there are records of 250 tagged trout being captured from the stream above the pond (Tables III and IV).

As noted, less effort was expended in fishing Wilmot Estuary than the pond (Tables V and VI). However, both the highest and lowest rates of capture, considered on a monthly basis, were observed for the estuary. The average

TABLE V. Creel census records for Wilmot Pond.

Year and month	Number caught	Rod-hours	Per rod-hour	Number of rods	Per rod	Number of successful rods
1956						
May (3–31)	148	114	1.3	40	3.7	39
June	294	334	0.9	111	2.6	73
July	309	304	1.0	142	2.2	55
Aug.	492	391	1.3	176	2.8	95
Sept. (1–15)	162	112	1.5	57	2.8	37
	1405	1255	1.1	526	2.7	299 (57%)
1957						
Apr. (15–30)	308	499	0.6	177	1.7	81
May	582	495	1.2	197	3.0	110
June	480	420	1.1	199	2.4	105
July	378	384	1.0	136	2.8	73
Aug.	199	354	0.6	116	1.7	49
Sept. (1–15)	24	53	0.5	12	2.0	6
	1971	2205	0.9	837	3.4	424 (51%)
1958						
Apr. (15–30)	578	774	0.8	283	2.0	114
May	202	328	0.6	162	1.2	38
June	546	425	1.3	182	3.0	93
July	294	314	0.9	169	1.7	65
Aug.	195	312	0.6	139	1.4	50
Sept.	139	128	1.1	66	2.1	29
	1954	2281	0.9	1001	2.0	389 (39%)
1956–58	5330	5741	0.9	2364	2.3	1112 (47%)

TABLE VI. Creel census records for Wilmot Estuary.

Year and month	Number caught	Rod-hours	Per rod-hour	Number of rods	Per rod	Number of successful anglers
1956						
May (3–31)	90	45	2.0	22	4.1	20
June	241	141	1.7	68	3.5	51
July	43	94	0.5	55	0.8	14
Aug.	22	21	1.0	20	1.1	7
Sept. (1–15)	11	9	1.2	10	1.1	4
	407	310	1.3	175	2.3	96 (55%)
1957						
Apr. (15–30)	24	77	0.3	38	0.6	5
May	196	202	1.0	96	2.0	56
June	480	221	2.2	144	3.3	81
July	10	49	0.2	36	0.3	8
Aug.	4	22	0.2	17	0.2	3
Sept. (1–15)	11	8	1.4	5	2.2	4
	725	579	0.9	336	2.2	157 (47%)
1958						
Apr. (15–30)	184	214	0.9	99	1.9	49
May	320	402	0.8	134	2.4	56
June	712	319	2.2	171	4.2	109
July	432	254	1.7	167	2.6	98
Aug.	40	72	0.6	50	0.8	13
Sept.	65	81	0.8	42	1.5	22
	1753	1342	1.3	663	2.6	347 (52%)
1956–58	2885	2231	1.3	1174	2.5	600 (51%)

rate of 2.1 trout per rod-hour for June was contemporaneous with the major upstream movements of trout (Fig. 3). Low rates in mid summer were associated with comparatively high water temperatures. (The water temperature in Prince Edward Island estuaries exceeds 20°C in summer (Medcof, 1939).) Above water temperatures of 20°C, brook trout tend to move into cooler waters. If they remain in waters over 20°C by choice or lack of opportunity to move out of them, they reduce their feeding activities and this is reflected in angling success (Smith and Saunders, 1958; Smith, 1960). In contrast to the situation in Wilmot Estuary, the water temperature of the pond remained below 20°C during the summer (Fig. 2). In turn, rates of capture in the pond remained in general comparatively good during that season.

About 50% of the anglers who fished Wilmot Pond and Estuary did not capture a trout and they accounted for 35% of the total fishing effort (Tables V and VI). These findings are not exceptional. Creel censuses often disclose a high proportion of unsuccessful anglers, emphasizing that angling is an inefficient way to capture fish. Rupp (1961) pointed out that the inclusion of the effort by unsuccessful anglers results in a statistic (catch per unit effort) "unsatisfactory to describe the fishing quality that a water is capable of providing". He advocated that a better measure of potential fishing quality could be derived by considering only the data for the more successful anglers, more precisely those for anglers who took about half of the total catch. Treating the data for the Wilmot area in this fashion, it is shown in Table VII that about 12% of the anglers took approximately 50% of the total catch at a rate of 2.9 trout per rod-hour. (These data are based on catches of 8 or more trout per fishing trip.) The rate of 2.9 trout per rod-hour is to be compared with average rates of 0.9 and 1.3 for the pond and estuary respectively when all of the effort was considered. Out of 3,538 angling trips (number of rods) recorded for the three angling seasons, 350 (10%) resulted in catches of 8 or more trout. The frequency of such catches, 138 out of the total of 350, was greatest in June, coincident with dominant upstream movement of trout. However, catches of this order were realized throughout the angling seasons, 99 in the spring months and 113 later in the summer. It is not inferred that only the more expert angler makes the largest catches. However, anglers who are knowledgeable about where, when and how to fish will doubtless, on the average, be the most successful. Thus, it is concluded that the effort of these better anglers showed that the quality of angling that could be realized in the Wilmot area was well above that indicated by the average success of all the anglers.

TABLE VII. Catch record for anglers that captured eight or more trout per fishing trip.

Year	Percentage of total number of anglers	Percentage of total catch	Catch per rod-hour
	I. Wilmot Pond		
1956	12	42	2.8
1957	11	50	2.5
1958	11	53	2.9
	II. Wilmot Estuary		
1956	10	38	3.6
1957	12	50	3.8
1958	14	49	2.9
	III. Pond and Estuary combined		
1956–58	12	49	2.9

MODES OF ANGLING AND CATCH

Fly-fishermen accounted for 13% of the total fishing effort, and for 17% of the fishermen. They captured trout at a rate of 1.2 per rod-hour, which was the same as the overall rate by all modes of angling in the pond and estuary. Sixty percent of the fly-fishing was done in July and August. The remainder of the fishing effort was expended almost entirely in still-fishing with bait, largely earthworms. Spinning (30 rod-hours) was negligible.

Size of Trout

Length frequencies among the trout angled from the pond are illustrated in Fig. 5. Comparison of Fig. 4 and 5 shows that length frequencies among the trout moving into and out of the pond and among those angled from the pond were similar. The majority of the angled trout had not, however, been involved in movements between fresh and salt water, at least so far as the trapping operations disclosed. Most of the angled trout, tagged or untagged, were ages I and II. Comparatively few older and larger trout were taken, again indicating that the Wilmot trout are short-lived, as has also been noted for the brook trout elsewhere (Hazzard, 1932; Shetter and Leonard, 1943; Smith, 1948; Smith and Saunders, 1958). Estimation of weight of trout (see below) revealed that only 1 in 48 of the angled trout was over half a pound, and that only 1 in 355 attained a weight of a pound or more (1 lb = 0.45 kg).

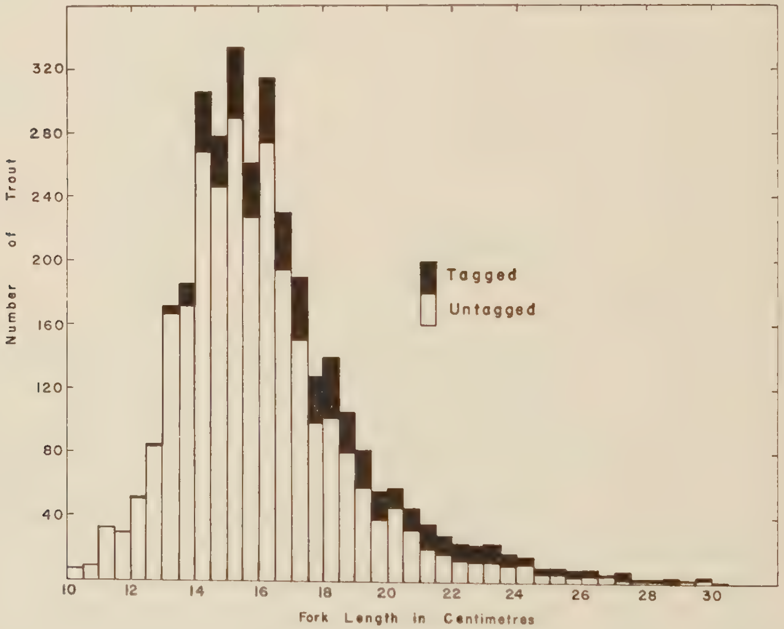

FIG. 5. Length frequencies among the brook trout that were angled from Wilmot Pond.

Yield of Trout by Weight from Wilmot Pond

The trout were not weighed when captured. Weight was estimated from the length-weight relationship, $W = 0.009515L^{3.097}$, established previously for Prince Edward Island brook trout and covering a comparable length range to that of the fish angled from Wilmot Pond. In this relationship, W is weight in grams and L, fork length in centimetres.

The yields in pounds per acre were 15.2 in 1956, 19.1 in 1957 and 23.1 in 1958 (1 lb/acre = 0.893 kg/ha). For comparison, the yearly average yield of trout from larger and deeper Montague Pond, Prince Edward Island, over a ten-year period, was 36.5 lb/acre (range, 22.4–44.8) (Smith, 1954).

Effect of Season Extension in 1958

In 1958, the angling season for brook trout in Prince Edward Island waters was extended two weeks to September 30. In this period, only 24 trout were caught from the Wilmot Estuary and 75 from the pond. Rate of capture was 1.2 fish per rod-hour, suggesting that quality of angling remained good. However, few anglers took advantage of the opportunity. The additional effort expended on the estuary was only 26 rod-hours and on the pond, 53 rod-hours. The effect of extending the angling season on catch was obviously minor.

POND AS A HOLDING AREA FOR TROUT

Intent in forming Wilmot Pond was to create a habitat which would hold trout in an accessible area and in which they would be readily available to anglers. Table V shows that reasonably good fishing was provided. Continued angling success to the end of the fishing seasons suggests, however, that the pond population was under-fished. (The maximum effort was 175 rod-hours per acre in 1958.) As previously noted, the pond embankment acted as barrier, if no more than temporarily, to trout moving upstream, and thereby was a probable factor in the favourable catches from the upper part of the estuary (Table VI). Data for catches from the area prior to pond formation are lacking. Opinion of local anglers supports judgment that population was larger and catch greater for the pond than for that stream area flooded in pond formation, and similarly for the upper part of the estuary after the embankment was built. The objective in forming Wilmot Pond was realized in good measure.

Trout ran from Wilmot Pond into the estuary in spring and autumn with few moving out between early June and late October (Fig. 3). Investigations at Ellerslie Brook, Prince Edward Island, also showed that trout which left the pond for the estuary did so largely in spring and autumn (unpublished data). With a trap between stream and pond, it was further shown that the trout entered the pond during these seasons as well. Without a trap between stream and pond at Wilmot, time of entrance into the pond was not documented. However, it would appear likely that the trout also preponderantly entered Wilmot Pond during spring and autumn, with only a portion of them leaving the pond at those times. A large proportion of the untagged trout angled from Wilmot Pond were age I, indicating no long term of residence in the pond (Fig. 5). They probably moved down into the pond during the spring. It was not to be expected that most of these trout would run from the pond into the estuary. Smith and Saunders (1958) determined over a four-year period that only about 17% of the trout in Ellerslie Brook that reached age I and a length of 12–13 cm ran to the estuary. The majority of trout lived and died in freshwater. When a pond was formed on Ellerslie Brook, still fewer trout ran to salt water (FRB, 1961). Ellerslie Pond, and doubtless Wilmot Pond in a similar manner, held a good many trout that moved downstream by providing additional and suitable living space in fresh water.

Of particular interest to the anglers in forming Wilmot Pond was the possibility of holding and making readily available more of the sea-run trout upon their return to freshwater. The largest brook trout taken in the Prince Edward Island area are usually sea-run individuals, and this was the basis for the particular interest. However, it was found at Wilmot, as elsewhere in the area, that the trout are short-lived, and large specimens are relatively few in the population (Fig. 4 and 5). During the study at Wilmot, 5,022 trout were tagged when they moved upstream into the pond during the angling seasons; 529 were tagged after the angling seasons had closed (Table III). In addition, 639 trout that had been tagged when leaving the pond, re-entered it (Table IV). Of the total of tagged trout that entered the pond, 766 (12%) were taken from the pond by anglers. This number of tagged trout represented 14% of the total catch (5,330) from the pond. There are also records of anglers capturing 115 tagged trout from the estuary after a second movement by these fish downstream, and 250 from the stream above the pond. It is to be noted again that none of the trout tagged in 1956 was captured either in the traps or by anglers in 1958.

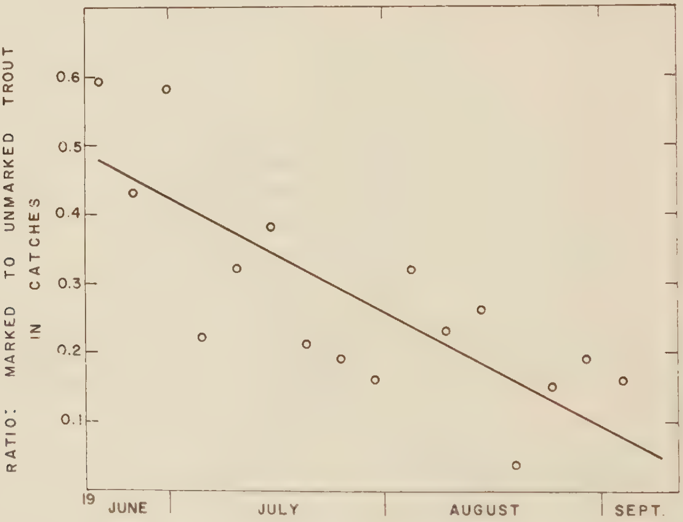

FIG. 6. Ratio of marked (tagged) to unmarked trout in anglers' catches from Wilmot Pond during angling season of 1956. Ratios calculated on catches during 5-day intervals.

The ratio of tagged to untagged trout in the anglers' catches from the pond declined with advance of the angling season (Fig. 6). (Fig. 6 is based on data for 1956 when these were uncomplicated by carry-over of tagged trout from the previous year.) Data in Table VIII show that the actual number of tagged trout caught in Wilmot Pond also declined within short periods after entry, although tagged trout continued to contribute to the catches until the end of the angling season. Among possible reasons for the above observations, a fairly rapid transit of the pond into the tributary stream by many, if not the majority,

TABLE VIII. Number of trout moving upstream into Wilmot Pond in June and July, and the number of these subsequently caught by anglers in the pond.

Year and month of entry	Number entering pond	Number captured by anglers during intervals after entry					Total caught
		1st week	2nd week	3rd week	4th week	Remainder of angling season	
1956							
June	1556	50	37	8	14	75	184
July	582	3	6	9	7	23	48
1957							
June	1365	58	24	10	11	49	152
July	420	3	2	2	1	7	15
1958							
June	1187	40	17	10	5	30	102
July	472	8	1	1	0	18	28
1956-58							
June	4108	148	78	28	30	154	438
July	1474	14	9	12	8	48	91

of the tagged trout is advanced as the most plausible. The incomplete creel census in the tributary disclosed capture of tagged trout in this area within a few days after upstream entry into the pond. The trout here under discussion are mainly those in the dominant upstream runs in June and July (Fig. 3). These are not viewed as spawning runs, but rather as indicative of response on the part of the trout to more favourable living conditions (Smith and Saunders, 1958).

Apparently Wilmot Pond functioned imperfectly as a holding area for those trout that moved upstream from the estuary. Also 2,578 trout moved out of the pond during the period of investigation (Table IV). Presumably, if more trout had been held, or at least delayed longer in movement up- and downstream, the pond would have been a more favourable angling area than was experienced. Temperature of water in the pond was suitable for trout (Fig. 2). Dissolved oxygen content and pH values were also suitable (Table I). Trout foods were in good supply (Table II). However, as noted above, a large proportion of the pond area has shallow water. Brook trout are secretive, and an important factor in the carrying capacity of freshwaters for trout is cover, either provided by depth of water or hiding places in shallow waters (Saunders and Smith, 1962). Comparing the situation and observations at Wilmot Pond with those in other Prince Edward Island ponds is informative. A 23-acre pond on the North Montague Stream, with maximum and mean depths of approximately 20 and 8 ft, respectively, held downstream-moving trout sufficiently well to provide yields of 22 to 45 lb per acre at rates of capture from 1.4 to 2.5 per rod-hour over a 10-year period (Smith, 1954). North Montague and Wilmot Streams are comparable in size. A 5-acre pond on Ellerslie Brook, a much smaller stream than either of the above, but with 34% of its area with water depths over 5 ft, effectively held upstream-moving sea-run trout for good cropping by anglers. In the years 1953–54, of 1,558 tagged sea-run trout in the pond, 63% were angled, 9% moved up into the tributary stream, and 11% again moved downstream (unpublished data). A general observation, but not well documented, is that shallow artificial Prince Edward Island ponds are poor to mediocre fishing areas for trout. These ponds may have been shallow when formed, or originally of suitable depth but later silted in. From what is known, it is concluded that Wilmot Pond would have held more trout to provide better angling if more of the pond area had had adequate depths for trout cover.

SUMMARY

1. A 13-acre pond was formed at the head of tide on the lower reaches of Wilmot Stream, Prince Edward Island, by building an embankment across the stream valley. Discharge from the pond is by an artificial channel around one end of the embankment. The objective in forming the pond was to provide an accessible area which would hold brook trout moving between stream and estuary for greater availability to anglers.
2. Trout moved freely between pond and estuary via the artificial outlet. Dominant upstream movements were in June and July, with lesser numbers in autumn; downstream in April and May, and again in the autumn. Few trout moved in or out during the summer.
3. In three angling seasons, 1956–58, fishermen cropped 5,330 trout from the pond and 2,885 from the upper stretches of the estuary at rates of 0.9 and 1.3 fish per rod-hour respectively. Approximately 50% of the total catch was made by 12% of the anglers at a rate of 2.9 trout per rod-hour.
4. Wilmot brook trout were short-lived. Trout moving into and out of the pond, as well as those angled from the pond, were preponderantly ages I and II.
5. Water temperature, dissolved oxygen content, pH value and supply of food are favourable for trout in the pond. The mean depth of water is 3½ ft, with 80% of the pond area with water less than 5 ft in depth. Although good angling was experienced after pond formation, the pond functioned imperfectly as a habitat and holding area for brook trout. Evidence from the Wilmot study, corroborated by findings at other Prince Edward Island ponds, indicated shallowness of water as the important habitat deficiency in holding trout, and that the deficiency curtailed better angling success in the pond.

ACKNOWLEDGMENTS

Field operations were under the immediate supervision of Mr Cyril Williams. The Prince Edward Island Department of Industry and Natural Resources provided the services of a resident creel-census taker. The assistance of Miss Mary Holmes in the laboratory is gratefully acknowledged. Messrs J. W. Saunders and C. R. Hayes also assisted in the program. Messrs P. W. G. McMullon and F. B. Cunningham prepared the figures.

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Organogenesis of the Opercular Apparatus in *Salvelinus fontinalis* (Mitchill)[1,2]

By L. R. Day

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

The opercular fold in *Salvelinus fontinalis* (Mitchill) begins as a bulging, outward and backward, of the undifferentiated dorsally-packed mesenchymal tissue of the hyoid arch in embryos of 6.0–6.5 mm total length. From 6.5 to 9.0 mm, backward growth takes place although no gill arches are covered. The epithelium of the opercular anlage is 2- to 3-layered laterally and 1- to 2-layered with smaller nuclei medially. From 9.0 to 14.0 mm, i.e. hatching, the membranous lateral opercular and ventral branchiostegal portions extend posteriorly to cover the four gill arches. Ossification commences in the opercle, the jaws and the pectoral girdle. The epithelium which has scattered goblet cells is 3- to 4-layered antero-laterally, 1- to 2-layered postero-laterally and one cell in thickness medially. From 14.0 to 30.0 mm length ossification of the skeletal elements of the opercular apparatus takes place. The musculature of the operculum is complete at hatching.

INTRODUCTION

The role played by the opercular apparatus is a very important one in Teleostomi where the mechanism for gill breathing reaches its highest degree of development among Pisces. It is necessary in respiratory and feeding processes and especially as a protection for the gills.

As far as could be determined records of the organogenesis of the opercular apparatus are lacking in the literature. This paper presents the results of a detailed examination of the origin and development of the gill cover in *Salvelinus fontinalis*.

MATERIAL AND METHODS

The embryological material used in the following study was obtained from two series of trout embryos and larvae collected by the Fisheries Research Board of Canada. The first series from the Saint John Hatchery included weekly samples taken from the time of fertilization of the eggs, November 6, 1934 until August 9, 1935 at which time the trout attained a length of 40 mm. Bouin's fixing fluid was used until June 21 after which preservation was effected in formalin. The second series was collected daily at the Birch Cove Hatchery, Charlotte County, N.B., from November 7, 1939 until May 14, 1940. Preservation was effected in Davidson's glycerine-formalin-acetic acid mixture. In addition trout larvae (hatching to complete absorption of yolk) and fry were obtained at weekly intervals from April 6, 1940 to June 21, 1940 from the Saint John Hatchery and preserved in 95% alcohol for subsequent bone staining.

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[1] Received for publication August 30, 1962.

[2] This paper is based on a thesis accepted by the University of Western Ontario in partial fulfilment of the requirements for the degree of Master of Arts.

J. Fish. Res. Bd. Canada, 20(2), 1963.
Printed in Canada.

The gross structure of the gill arches and opercular apparatus was studied under a binocular microscope. Measurements of the backward growth of the operculum were made with a micrometer eyepiece. Both coronal and transverse sections of the head region were prepared at a thickness of 10μ by the dioxan method with Erhlich's haematoxylin and triosin staining. A camera lucida was used for preparing the drawings of lateral and ventral view of the entire specimens, a micro projector for outlining the coronal sections.

The usual technique of clearing with potassium hydroxide and subsequent staining with alizarin red and preservation in glycerine was followed in tracing the ossification of the various bony elements in the opercular apparatus.

OPERCULAR GROWTH

As the operculum or gill cover during early development gradually extends backwards to cover the gill arches, its linear growth can be recorded by measurements.

TABLE I. Average weekly measurements of *Salvelinus fontinalis* (Mitchill) embryos and fry to show opercular growth.

Age	Total length	Nose to fin	Eye to operculum	Operculum to fin	Temperature
weeks	*mm*	*mm*	*mm*	*mm*	°*C*
6	4.5	1.65	0.56	0.66	0.56
7	5.0	1.71	0.56	0.49	0.56
8	5.5	1.81	0.52	0.46	0.56
9	5.5	1.81	0.49	0.52	0.56
10	6.0	1.81	0.49	0.56	0.56
11	6.0	1.84	0.49	0.59	0.56
12	6.5	1.98	0.49	0.39	0.56
13	?	?	?	?	0.56
14	8.5	1.91	0.49	0.36	0.56
15	9	2.24	0.32	0.33	0.56
16	9.5	2.14	0.59	0.26	0.56
17	9.5	2.14	0.72	0.19	0.56
18	10	2.14	0.72	0.16	0.56
19	10.5	2.37	0.75	0.19	0.56
20	12	2.47	0.82	0.09	0.56
21	12	2.37	0.99	0.06	0.56
22	12.5	2.47	1.02	0.06	0.56
23	13.5	2.57	1.05	0.13	0.56
24	14.5	2.77	1.22	0.09	3.6
25	15.5	2.97	1.32	0.06	7.2
26	19	3.63	1.65	0.00	8.6
27	21	4.29	2.14	0.00	10.3
28	22	4.55	2.31	0.00	11.7
29	23	4.95	2.31	0.16	14.1
30	27	5.44	3.06	0.26	19.1
31	29	6.10	3.30	0.16	17.8
32	29	5.94	3.30	0.00	15.6

Owing to the fact that the hyoid arch from which the gill cover develops has no fixed external landmark it cannot be utilized in making measurements of opercular lengths. Therefore it is necessary to use as landmarks structures such as the eyes and the pectoral fins which remain in a relatively fixed position throughout development.

Three measurements (Table I) as follows were made for the series of embryo and fry collected weekly from November 1934 to June 1935 at the Saint John Hatchery: first, from the posterior margin of the eye to the posterior edge of the operculum; second, from the posterior edge of the operculum to the base of the pectoral fin; and third, from the anterior tip of the nose to the base of the pectoral fin. These were plotted against the total length–age relationship (Fig. 1) and show the rate of growth and backward extent of the operculum. Each item in Table I and Fig. 1 represents the average length as calculated from measurements recorded for at least 10 specimens. A record of the temperature through which this series of embryos and fry has passed is also included, since this is essential to a correct interpretation of certain of the data.

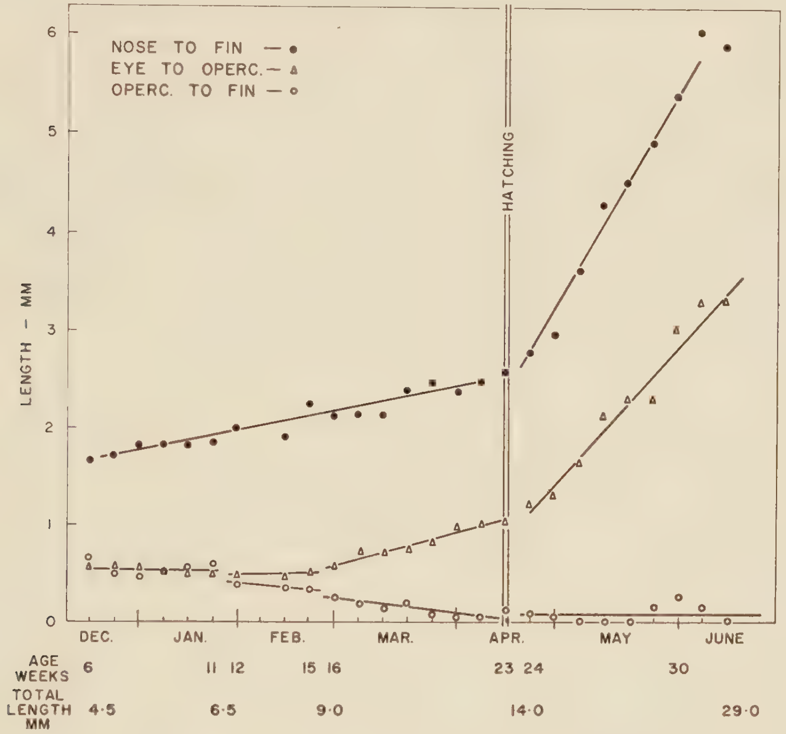

FIG. 1. Development and growth of the opercular apparatus in *Salvelinus fontinalis* (Mitchill).

Reference to Table I and Fig. 1 shows that the nose–fin distance increases gradually until the twenty-third week, i.e. the time of hatching. A sudden rise in temperature immediately following this is probably responsible for the subsequent marked acceleration in growth.

The eye–operculum distance and the operculum–fin distance may be considered together as the two are inversely related. From the sixth to the eleventh week (4.5–6.5 mm total length) the posterior margin of the hyoid arch remains the halfway mark between the posterior edge of the eye and the pectoral fin. The four gill arches are also being cut off from the undifferentiated mass of tissue posterior to the preformed hyoid arch during this time. Between the eleventh and the fifteenth week (6.5–9.0 mm total length) the operculum begins as a fold on the posterior lateral surface of the hyoid arch. However, the backward growth is relatively slow. Microscopic examination reveals differentiation within the hyoid arch rather than extensive opercular elongation. The operculum or gill cover, during the following 8 weeks (9.0–14.0 mm total length), i.e. immediately prior to hatching, extends rapidly caudad to cover in succession the four gill arches before hatching. Following hatching, there is a rapid increase in temperature, an enlargement of the structures already formed, and the rate of growth of the operculum roughly parallels that of the nose–fin region.

In summarizing, four phases of opercular development can be recognized: first, the formation of the hyoid and branchial arches (4.5–6.5 mm total length); second, the appearance of the operculum and specialization of the hyoid arch (6.5–9.08 mm total length); third, the backward growth of the operculum to cover the four branchial arches, prior to hatching (9.0–14.0 mm total length); and fourth, the post-hatching period of growth.

THE EMBRYOLOGICAL DEVELOPMENT OF THE OPERCULAR APPARATUS

I. Development of the Branchial Arches

1. 4.5 to 5.0 mm stage (age 6 weeks, fig. 2)

The unhatched embryo adheres to the yolk and extends in a narrow band over one third the circumference of the yolk sac. The head and pharyngeal regions occupy one third of the body length. The three brain vesicles are developed. Anteriorly, the hind-brain is characteristically folded to form the cerebellum and the fourth ventricle is restricted to a longitudinal slit. The optic cup is differentiated and the lens anlage is cut off from the ectoderm. The choroid fissure is apparent externally as a wide slit ventral to the lens. The auditory vesicle is prominent, due to the thin transparent ectodermal covering, in the region lateral to the third, fourth, and fifth neuromeres. A pair of olfactory thickenings are present ventrally between the eyes.

Behind the eyes on each side and extending ventrally in arches are two dense concentrations of mesenchyme. The anterior concentration is the anlage of the mandibular arch and the posterior one of the hyoid.

The indentation which is the line of separation between the arches is directly ventral to the division between the mid- and hind-brains. The mouth is occluded and is situated mid-ventrally posterior to the eye. The funnel-shaped heart lies against the yolk mid-ventrally between the two hyoid concentrations.

Posterior to the hyoid concentrations on each side is a deep indentation extending from the mid-ventral line laterally and dorsally to the mid-lateral surface. This is an indication of the location of the first branchial slit and lies directly ventral to the anterior end of the auditory vesicle. The anlage of the first branchial arch is a cellular concentration extending downward and forward to the thin mid-ventral region of the pharynx at the level of the auditory vesicle. Below the posterior end of the auditory vesicle is an indication of the second branchial slit. The remaining pharyngeal region to the level of the pectoral fin buds consists of a ventro-lateral undifferentiated cellular plate, the branchial arch anlage. Posterior to the latter, the pharynx is constricted to a narrow tubular oesophagus.

The pectoral fin buds appear as transparent masses free from the body, lateral to the posterior and of the medulla oblongata.

2. 5.0 mm STAGE (AGE 7 WEEKS, FIG. 3)

The head region of this embryo has increased in width and the caudal region is now free from the yolk sac. The three brain vesicles are more clearly defined. The cerebellar fold of the hind-brain is greatly extended while the fourth ventricle is now V-shaped and tapers to a narrow slit at the level of the pectoral fins. The initial semicircular canal and otolith differentiation can be observed in the auditory vesicle. The pharynx and mouth are occluded. The mandibular and hyoid regions show no advancement over the 4.5 mm stage. The first two branchial slits are more pronounced while a second branchial arch has been cut off from the branchial anlage just posterior to the first one.

3. 5.5 mm STAGE (AGE 9 WEEKS, FIG. 4 AND 5)

This stage shows advancement over the 5.0 mm stage in its external appearance. The head region is wider and the caudal tapering is therefore more pronounced. The meso-metencephalic fold of the brain region extends more laterally and ventrally. Posteriorly the fourth ventricle is widened and has a transparent epithelial covering and the pectoral fin anlage are now dense, opaque concentrations extending lateral to the embryo at the posterior pharyngeal region.

The mandibular arches viewed from the ventral surface appear as two horseshoe-shaped concentrations curved distally on each side of the mid-ventral line. The most anterior part of each arched concentration is the maxillary portion of the mandibular arch while the more posterior is the mandibular portion of the first visceral arch. The thin transparent region enclosed by the arches is the mouth which is still occluded.

Three pairs of branchial arches have been cut off from the branchial anlage on each side. The ventral ends of these are joined to heavy mesenchymal concentrations which extend along each side of the mid-ventral line from the hyoid arch posteriorly to the oesophageal constriction. The first branchial slit has become more conspicuous laterally and ventrally because the first branchial arch has migrated some distance from the hyoid arch. The other two branchial arches are closely adherent to the first which is the largest.

4. 6.0 mm STAGE (AGE 11 WEEKS, FIG. 6 AND 7)

In this stage the embryo has become raised off the surface of the yolk because of an increase in the body depth. The head as far back as the hyoid arch and the caudal region for approximately one third of the body length are free from the yolk. The body occupies approximately one half the yolk circumference.

The mouth is now open and located ventrad at the level of the posterior margin of the eyes. The pharynx is patent to the first gill arch. The branchial anlage has now been divided into four branchial arches. A fifth arch which will be non-functional in the adult makes up the most posterior portion in the pharynx just anterior to the constricted oesophagus. From the ventral aspect, the branchial region appears narrower than the mandibular and hyoid regions which bulge laterally.

Coronal sections of a specimen of this size show that hyoid and branchial arches are outlined by a single row of low columnar epithelial cells. The nuclei of these are all elongated, pointed outward giving a palisade effect. Inside that palisaded extremity of these arches there is an undifferentiated mass of mesenchymal cells with many nuclei. Clear spaces in the central mass of the hyoid and first branchial arches are the lumina of the branchial vessels.

II. INITIAL DEVELOPMENT OF THE OPERCULAR APPARATUS

5. 6.5 mm STAGE (AGE 12 WEEKS, FIG. 8, 9 AND 10)

The appearance of the embryo is much the same as described for the 6.0 mm stage. The head and pharynx have increased in depth and taper to a narrow body region. Auditory vesicle has semicircular canals already visible and extends on the latero-dorsal surface from the middle of the hyoid arch backward to the second branchial arch.

Specimens of this stage exhibit the initial appearance of an opercular structure. The hyoid arch has grown caudally outward and downward from the lateral posterior region to cover a small portion of the upper anterior extremity of the first branchial slit. In coronal section a mesenchymal concentration of the central portion of the hyoid arch narrowed laterally and posteriorly as a blunt projection inside the conforming palisade layer.

The hyoid and first branchial arches have a wide cleft and meet lateral to the mid-ventral line establishing the first indication of the basibranchial region. The first branchial arch is the longest and widest while the fourth is shortest and thinnest.

6. 7.0 to 7.5 mm STAGE (AGE 13 WEEKS, FIG. 11–15)

At this stage the scattered black pigmentation has appeared around the outer margins of the optic cups. The right and left sides of the maxillary and mandibular portions of the first visceral arch have fused in the mid line and now bound the mouth opening anteriorly and posteriorly respectively.

The hyoid arch continues to bulge laterally and posteriorly thus creating an opercular flap. Coronal sections reveal medial to the hyoid arch, the presence of a sub-hyoidean chamber as an extension of the first branchial slit forward to the anterior limits of the hyoid arch.

The blood supply to the hyoid and mandibular arches is well established.

7. 8.0 to 8.5 mm STAGE (AGE 14 WEEKS, FIG. 16 AND 17)

These specimens show heavy black pigmentation in the eye region. The horoid fissure externally is less wide. The mouth opening is large and rectangular and has taken up a more anterior position on the ventral surface of the head. The mouth cavity is now large and more exposed.

The pharynx is still occluded in the region of the fourth branchial arch. The first three gill slits are open to the pharynx. The branchial arches in the ateral and ventral regions have begun their characteristic forward flexion. The whole mid-ventral region is being displaced forward due to the anterior migration of the mouth which now comes to be partially closed by the elongating mandibular parts.

The hyoid arch is losing its undifferentiated condition. Its posterior ateral edge has elongated leaving a hyoidean portion and an opercular portion which are readily observed in coronal sections of the 8.5–9.0 mm stage. There s thus formed a sub-hyoidean and a subopercular chamber. The opercular flap portion of the hyoid has extended backwards dorsally and laterally, and ventrally it is approaching the first branchial arch. Histologically, the lateral surface of the hyoidean and opercular portions consists of an epithelium which has become 2- or 3-layered but appears to be syncytial. The surface nuclei tend to be flattened. The medial surface has a much thinner epithelium of 1 to 2 layers. The surface layer is flattened and the nuclei are smaller in the opercular portion but the underlying layer has palisaded nuclei in the hyoidean portion.

8. 8.5 to 9.0 mm STAGE (AGE 15 WEEKS, FIG. 18, 19 AND 20)

In this embryo there has been increased definition of the mouth cavity. The posterior corners are pulled backwards and folds are developing between the maxillae and mandibulae. An infolding marks the separation between the mandibular and hyoid arches along the ventral surface. Further widening of the head and first two visceral arches caused their outward extension over the pharyngeal region on each side.

The hyoid differentiation into a hyoidean and an opercular portion is more pronounced. The opercular flap has become thinner and covers the first branchial slit. The operculum and hyoid are being pulled forward ventrally along with the mandibula. The hyoid and operculum are well supplied with blood by a hyoidean vessel. The latter passes over a medially placed concentration of mesenchymal tissue which will differentiate into the hyomandibular cartilage. The developing pseudobranch may be observed in coronal sections at the extreme posterior end of the mandibular arch in the sub-hyoidean cavity. It appears as a bulging of a double row of palisaded nuclei.

III. SUBSEQUENT GROWTH OF THE OPERCULAR APPARATUS

9. 9.5 to 10.0 mm STAGE (AGE 17 WEEKS, FIG. 21)

In embryos of this stage the pharynx is still occluded between the fourth branchial arch and the oesophageal constriction. Precartilage has differentiated from the mesenchymal concentrations in the hyoid arch to form the hyomandibular and hyoid bar and in the mandibular arch forming Meckel's cartilage. Aggregations of mesenchyme medial to the branchial vessels in each branchial arch will become the ceratobranchial and basibranchial cartilages.

The hyoid and mandibular arch have been drawn further anteriorly in the mid-ventral region. The mouth is being progressively closed from its posterior margin, the mandibular symphysis. The branchial arches are pulled downward and forward and consequently the leaf-like operculum which now covers the first branchial arch latero-ventrally still has its greatest caudad extent at the point of dorsal union with the lateral body wall.

10. 10.0 to 11.0 mm STAGE (AGE 19 WEEKS, FIG. 22 AND 23)

The body of the embryo in this stage completely encircles the yolk sac. Black pigmentation is scattered along the dorsal and lateral surfaces but is concentrated in the eye region. The eyes are protruding and the olfactory organs have migrated from their former mid-ventral position between the eyes to the anterior end of the head. The hind-brain remains smaller in comparison with fore-brain and mid-brain regions. The auditory organs have sunken further below the surface. The pectoral fins which are fan-shaped and directed upright have a transparent terminal margin and are now closely applied to the posterior pharyngeal region. Laterally and dorsally the thin opercular flap covers the first two branchial arches. Its mid-ventral junction with the basihyal is pulled anteriorly due to the migration of the mouth. In coronal section further histological differentiation of the opercular and hyoid portions has taken place. The lateral epithelium has developed goblet cells. The mesenchyme of the operculum is loosely arranged under the outer epithelial layers. The pseudobranch has an outer layer of palisaded nuclei while the inner palisaded layer has become disrupted. Precartilage has become true cartilage only in the parachordal.

11. 11.0 to 12.0 mm STAGE (AGE 21 WEEKS, FIG. 24, 25 AND 26)

In embryos of this stage the mouth, pharynx and branchial slits are all open forming a continuous passage. Black pigmentation has increased around the eyes and over the dorsal part of the brain and body region. The ventral aorta leads into the mid-ventral region between the first two gill arches having been displaced posteriorly from its former positions between the hyoid junctions.

The operculum is still lamellar and transparent but well supplied with blood by the hyoidean vessel. The first three branchial arches can readily be observed through it. Dorso-laterally it extends farthest pectorad.

Just posterior to eye, muscular tissue has been differentiated from mesenchyme to form the adductor mandibularia muscle.

12. 13.0 mm STAGE (AGE 22 WEEKS, FIG. 27)

The mouth has become closed by forward extension of the mandibular arches. A groove between the mandibular and hyoid arches passes outward and backward from the mid-ventral region. Caudad to this groove along the posterior margin of the hyoid the undifferentiated branchiostegal portion of the opercular apparatus has become apparent. The opercular portion of the opercular apparatus continues its backward extension covering all four branchial arches and leaving only the last branchial slit exposed laterally. The greatest caudad extent of the opercular apparatus is dorso-laterally where it overhangs all the branchial arches with its posterior margin passing both anteriorly and ventrally to the basihyal region.

In coronal section, the hyomandibular cartilage appears flattened longitudinally in the dorsal region and elongated ventrally. A concentration of mesenchyme just under the lateral epithelium of the operculum and posterior to the dorsal part of the hyomandibular cartilage is the anlage of the membranous opercular bone.

The lateral epithelium of the operculum varies from 3 to 4 layers in thickness at the level of the hyomandibular cartilage and is reduced to 1 to 2 layers at its posterior lateral extremity. Just lateral to the posterior edge of the hyomandibular cartilage, the peculiar bud-shaped sensory organs of the preopercular or hyomandibular canal of the lateral line system have appeared in the epithelium. The medial epithelium of the operculum is one layer in thickness and has a few scattered goblet cells. The pseudobranch is a three-lobed structure medial to the hyomandibular cartilage in the sub-hyoidean chamber. The epithelial layer of the first branchial arch is thrown into folds along the postero-lateral surface. These are the primary gill filaments and are most evident on the ventral margin of the arch.

13. 14.0 mm STAGE (AGE 23 WEEKS, FIG. 28 AND 29)

Specimens of this stage are just hatching. The mouth is now completely closed and has taken up a position with the maxillae reaching the anterior level of the eyes. The olfactory organs are now antero-dorsal to the mouth. The head and body pigmentation is dense dorsally, obscuring the brain and auditory organs.

The opercular portion of the opercular apparatus now covers all the branchial arches and slits laterally. Ventrally the branchiostegal flap extends backward and downward over the bases of the first 2 branchial arches. Mid-ventrally the basihyal region has been drawn forward and the ventral aorta now passes dorsally in the basibranchial region between the first and second branchial arches. The exposed basibranchial region is covered by the heart and ducts of Cuvier which extend out over the yolk surface.

The primary branchial filaments now appear as long epithelial folds on all the branchial arches. They have a capillary blood supply. Skeletal parts of the mandibular, hyoid and branchial arches are cartilaginous.

Evidences of the initiation of ossification in the mesenchyme of the opercular, maxilla and pectoral girdle are apparent in histological sections.

IV. OSSIFICATION OF OPERCULAR ELEMENTS

14. 15.0 mm STAGE (AGE 24 WEEKS, FIG. 30)

At this stage the embryo has hatched. The dorsal, caudal and anal fins form a continuous fold along the mid-dorsal and ventral lines. The pectoral fins have thickened bases and an upright fan-shaped terminal portion. The pelvic fin buds have made their first appearance at the posterior end of the yolk sac. The nostrils are present at the extreme anterior end of the head. Because of the bending of the head upward off the yolk at hatching the mouth is pulled open.

The branchial arches are flattened so that they lie close against each other. The branchial filaments are directed backwards in the branchial or subopercular chamber.

Examination of an alizarin red stained specimen revealed ossification of four caudal rays in the caudal fin. Ossification of the opercular begins at its articulation point with the hyomandibula and extends backward and downward forming a small triangular area whose posterior and ventral margins are irregular. In the upper jaw under the eyes a thin line of ossification indicates the maxillary bone and in the lower jaw, the dentary. In the pectoral girdle the dorsal portion of the cleithrum is ossified.

The muscles of the cheek and the opercular region are visible under strong transmitted light in cleared specimens as fibrils. They are as follows: the levator operculi muscle fibrils pass directly upward to the brain case from the dorsal edge of the ossified portion of the opercular; the dilatator operculi muscle fibrils pass dorsally and anteriorly from the anterior end of the ossified opercular; the adductor mandibulae muscle, a large muscle (cheek muscle), whose fibrils pass from the dorsal lateral surface of the hyomandibular cartilage to the mandible; the levator arcus palatini muscle, a large muscle with fibrils directed ventrally and caudally to disappear under the belly of the adductor mandibulae muscle; the adductor operculi muscle in the specimens examined was hidden at the posterior edge of the eye and the belly of the adductor mandibulae muscle. Its fibrils parallel those of the levator arcus palatini muscle (Fig. 30).

These muscles persist throughout development as the characteristic adult musculature (Fig. 31 and 37).

15. 18.0 mm STAGE (AGE 27 WEEKS, FIG. 31)

Specimens of this stage show a reduction in the size of the yolk sac and consequently the heart assumes a more horizontal position. The pectoral fins are very large being almost the size of the head. Black pigmentation is very dense on the dorsal regions of the head and body.

A second row of primary branchial filaments has developed as tiny outpouchings on each branchial arch anterior to and alternating with the first row. They are furthest developed on the fourth branchial arch. The opercular apparatus is thin and transparent and distinctly divided into a lateral opercular region and a ventral branchiostegal region.

Examination of specimens stained with alizarin red shows the ossification of 14 caudal fin rays, 8 dorsal fin rays, 4 anal fin rays and 4 pectoral fin rays. The ossification of the opercular now extends more caudad and ventrad. Directly ventral is a small area of ossification, the interopercular. Below this again is a stained sabre-shaped area, the tenth branchiostegal ray. The maxillary and dentary bones have increased in size. Posterior to the dentary the articulare bone is appearing. The post-temporal and supra-cleithrum of the pectoral girdle are ossified at the dorsal end of the cleithrum.

16. 19.0 mm STAGE (AGE 27 WEEKS, FIG. 32)

There are in these specimens 16 caudal fin rays, 5 anal fin rays, 8 dorsal fin rays. In addition premaxillary ossification has taken place anterior and dorsal to the maxillary bone. The ninth branchiostegal ray has begun ossification. All other bones ossified in the 18 mm stage have increased their areas.

On the branchial arches, secondary filaments have formed as transverse folds along the primary filaments. Branchial rakers have appeared along the anterior edge of each arch.

17. 20.0 mm STAGE (AGE 28 WEEKS, FIG. 33)

In the specimens studied, there were 19 caudal fin rays, 5 anal fin rays, 11 dorsal fin rays, 8 pectoral fin rays. Neural arches along the trunk and haemal arches near the anal fin are bony. The dorsal end of the notochord has acquired a bony encasement. The bones of the pectoral girdle already present in previous stages have increased in area. The hyomandibula is ossified near its articulation with the opercular. Bone has appeared in the ceratohyal of the hyoid bar, the quadrate, symplectic and hypurals.

Ossification of the opercular apparatus include branchiostegal rays 10, 9, 8 and 7. The subopercular appears as a stained area between the opercular and interopercular, the latter of which has ventral and caudal extensions.

18. 22.0 mm STAGE (AGE 29 WEEKS, FIG. 34)

Ossifications in specimens of this stage include 24 caudal fin rays, 11 anal fin rays, 13 dorsal fin rays, 10 pectoral fin rays and 6 pelvic fin rays.

The pigment pattern which gives the adult its name, speckled trout, is becoming more pronounced. Yolk absorption has continued until the depth of the yolk sac is only equal to the thickness of the body. A thickening, the adipose fin, has appeared in the fold joining the dorsal and caudal fins.

Ossification areas in the opercular apparatus have increased. The opercular has extended backward towards the margin of the opercular flap. The subopercular and interopercular have increased their bony extent. The preopercular has appeared as an elongated area of ossification anterior to the subopercular and the interopercular. A fifth branchiostegal ray has become bony as well as the ceratobranchials and rakers of all five branchial arches. Occipital and otic regions are gradually ossifying. The maxillary and dentary bones now bear teeth. A foramen for the hyomandibular branch of the facial nerve is enclosed by the bony hyomandibula.

19. 23.0 mm STAGE (AGE 30 WEEKS, FIG. 35)

In this stage ossifications include 27 caudal fin rays, 14 anal fin rays, 12 pectoral fin rays, 8 pelvic fin rays and 14 dorsal fin rays. The hypural bones of the tail are more numerous and are beginning to fuse. Neural and haemal arches are ossified anterior to the vent. The ribs and ventral halves of the vertebrae are bony. The premaxillary is toothed on its ventral margin.

There has been an increase in size of all opercular bones. The preopercular is perforated and is folded along its lateral surface. There are six branchiostegal rays. The opercular overlaps with its ventral edge the dorsal margin of the subopercular which also is overlapped ventrally by the interopercular.

20. 23.0 mm STAGE (AGE 30 WEEKS, FIG. 36)

All the yolk has been absorbed. The bones or ossification areas have all increased in size. There are 29 caudal fin rays, 14 anal fin rays. 14 dorsal fin rays, 12 pectoral fin rays and 8 pelvic fin rays. The fourth to tenth branchiostegal rays are present. The preopercular has become more folded and perforated along its lateral margin where the preopercular or hyomandibular branch of the lateral line system extends.

21. 25.0 mm STAGE (AGE 31 WEEKS, FIG. 37)

Specimens of this stage show a marked increase in bony structure. There are 13 pectoral fin rays, 31+ caudal fin rays and 8 branchiostegal rays. Bone invasion has taken place around the supraorbital, postorbital, preopercular and mandibular extensions of the lateral line system. Symplectic, quadrate bones and the pterygo-palatine arch are ossified. The ceratobranchial of the fifth branchial arch bears pharyngeal teeth. There is a ring of ossification around each vertebra anterior to the pelvic region.

22. 31.0 mm STAGE (AGE 35 WEEKS, FIG. 38)

The following structures are ossified: 14 pectoral fin rays, 14 anal fin rays, 43 caudal fin rays, 15 dorsal fin rays, the epihyal, the hypohyal, the interhyal, the pectoral girdle and the jugal, lachrymal, supraorbital, suborbital all around the lateral line extension. In the opercular apparatus nine branchiostegals are evident and increased ossification of preopercular, angular, articular and dentary around the lateral line extension. An enlargement of the ossified areas of all the elements of the opercular apparatus has taken place. The basibranchials are also ossified.

The musculature of the opercular apparatus resembles that present in the earlier stages except that it has increased in size and extent.

The adult condition of the operculum is very closely approached. The fleshy terminal flap of the opercular portion posterior to the region supported by the skeletal elements closes the branchial chamber completely as it lies against the pectoral girdle. The branchiostegal division lies against the musculature of the hyoid bar and closes the ventral branchial chamber.

23. 157.0 mm STAGE (FIG. 39 AND 40)

The adult external characteristics have been attained and internally ossification has been completed.

The hyoid arch has a number of ossification centers and is closely connected with the mandibular arch. The hyomandibula is a large bone which articulates with a shallow groove lined by cartilage and formed partly in the pterotic. The yomandibula is overlapped in front by the metapterygoid, while below it tapers. t is succeeded by a small area of unossified cartilage followed by the forwardly irected symplectic which fits into a groove in the quadrate. The distal portion f the hyoid arches is strongly developed. The most dorsal element is the nterhyal, a short bony rod, articulating dorsally with a patch of cartilage ntervening between the posterior part of the hyomandibular and the symplectic. he interhyal is united below with the apex of the triangular epihyal followed by he middle portion forming the ceratohyal. In front of this is the small hypohyal. he hyoid arches of the two sides are united by the large tooth-bearing glossohyal.

Attached to the lower surface of the hyoid arch are a series of 10 to 12 flat ranchiostegal rays. Each overlaps the one in front of it, the posterior being he largest. Behind the hyomandibula is a large bony plate formed of four large embrane bones. The anterior of these, the preopercular, is crescentic and at ts upper end is connected with a small supratemporal. Behind the upper part f the preopercular is the largest of the opercular bones, the opercular. Its lower dge overlaps the subopercular and both opercular and subopercular are partially overed by the interopercular. In front, the interopercular is in its turn overapped by the preopercular.

SUMMARY

1. The mandibular and hyoid arches are distinct in embryos of *Salvelinus ontinalis* (Mitchill) prior to the 4.5 mm stage at which time the first branchial rch is cut off from the branchial anlage. Subsequently, the second to fourth ranchial arches are defined by 6.5 mm stage.

2. The opercular fold appears as a bulging outward and backward of the ndifferentiated densely-packed mesenchymal tissue of the hyoid arch in mbryos of 6–6.5 mm. It is covered externally by a single layer of low columnar pithelium with palisade nuclei.

3. From stages 6.5 to 9 mm, backward growth takes place although no ill arches are covered. The first branchial slit widens and differentiation of the yoid arch into the hyoid proper and the opercular anlage creates a sub-hyoidean nd a subopercular chamber. The lateral surface of the opercular anlage is overed by an epithelium which has become 2- or 3-layered but appears to be yncytial. The surface nuclei are flattened. The epithelium of the medial urface is much thinner consisting of 1 to 2 layers with small nuclei.

4. In embryos of 9 to 14 mm, i.e. hatching, the membranous opercular ap is now divisible into a lateral operculum proper and a ventral branchiostegal ortion. The operculum proper extends posteriorly to cover in succession the our gill arches. The branchiostegal portion extends backward and forward ver the bases of the first two branchial arches. Concentrations of mesenchyme ndicate the future positions of the bony elements of the opercular apparatus. ssification itself has commenced in the opercular, the jaws and the pectoral irdle. The lateral epithelium of the operculum varies from 3 to 4 layers in ickness at the level of the hyomandibular cartilage and is reduced to 1 to 2

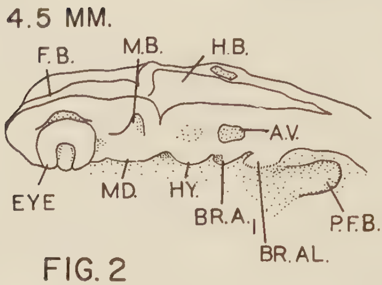
4.5 MM.
F.B.
M.B.
H.B.
A.V.
EYE
MD.
HY.
BR.A.1
BR.AL.
P.F.B.

FIG. 2

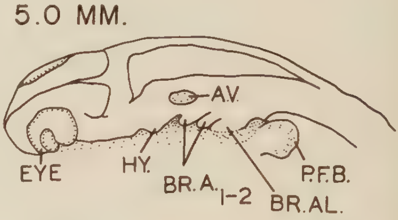
5.0 MM.
A.V.
EYE
HY.
BR.A.1-2
P.F.B.
BR.AL.

FIG. 3

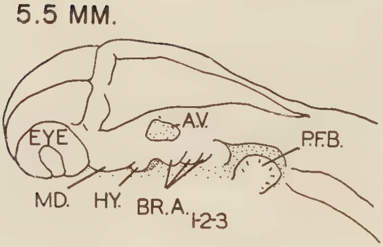
5.5 MM.
EYE
A.V.
P.F.B.
MD.
HY.
BR.A.1-2-3

FIG. 4

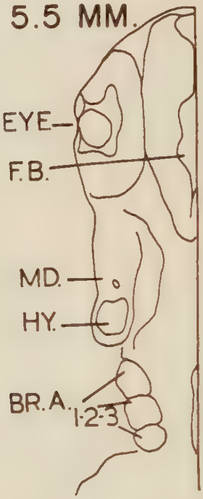
5.5 MM.
EYE
F.B.
MD.
HY.
BR.A.1-2-3

FIG. 5

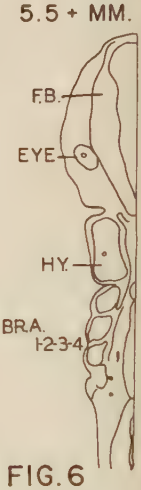
5.5 + MM.
F.B.
EYE
HY.
BR.A.1-2-3-4

FIG. 6

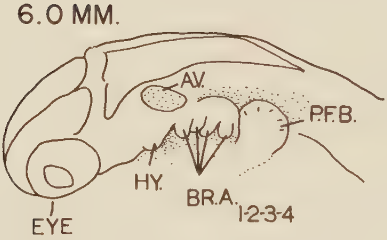
6.0 MM.
A.V.
P.F.B.
HY.
BR.A.1-2-3-4
EYE

FIG. 7

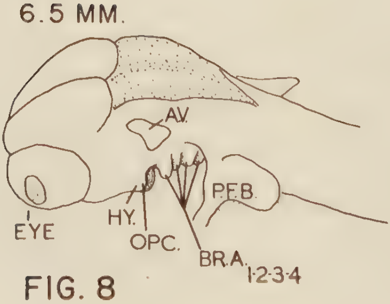
6.5 MM.
A.V.
P.F.B.
EYE
HY.
OPC.
BR.A.1-2-3-4

FIG. 8

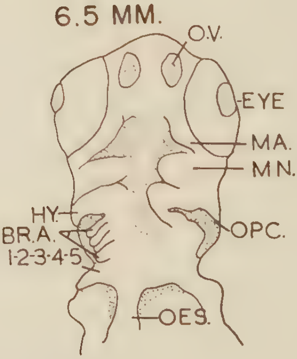
6.5 MM.
O.V.
EYE
MA.
MN.
HY.
BR.A. 1-2-3-4-5
OPC.
OES.

FIG. 9

FIGURES 2–9

Camera lucida and microprojections of embryo trout, whole mounts and coronal sections

FIG. 2. Lateral aspect of 4.5 mm embryo showing the hyoid and first branchial arch.

FIG. 3. Lateral aspect of 5.0 mm embryo showing the first two branchial arches.

FIG. 4. Lateral aspect of 5.5 mm embryo showing the first three branchial arches.

FIG. 5. Coronal section through the pharyngeal region of a 5.5 mm embryo showing the hyoid and first three branchial arches.

FIG. 6. Coronal section through the pharyngeal region of 5.5+ mm embryo showing the hyoid and first four branchial arches.

FIG. 7. Lateral aspect of 6.0 mm embryo showing the hyoid and first four branchial arches.

FIG. 8. Lateral aspect of 6.5 mm embryo showing the initial appearance of the opercular fold.

FIG. 9. Ventral aspect of a 6.5 mm embryo dissected from yolk and showing the initial appearance of the opercular fold.

Abbreviations. — A.V., auditory vesicle; BR.A. $_{1\text{-}5}$, first to fifth branchial arch; BR.AL., branchial anlage; EYE, developing eye; F.B., fore-brain; H.B., hind-brain; HY., hyoid arch; M.A., maxillary portion of the mandibular arch; M.B., mid-brain; MD., mandibular arch; P.F.B., pectoral fin bad; M.N., mandibular portion of the mandibular arch; O.P.C., opercular fold; O.V., developing olfactory organs.

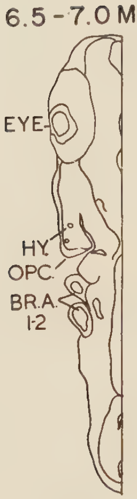
6.5 - 7.0 MM.
EYE
HY.
OPC.
BR.A.
1-2

FIG. 10

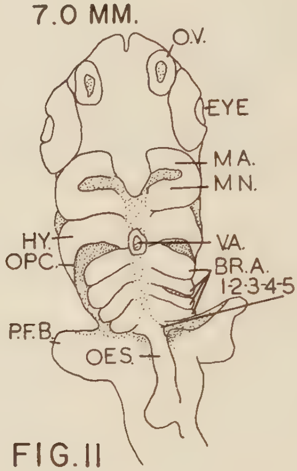
7.0 MM.
O.V.
EYE
M.A.
M.N.
HY.
OPC.
V.A.
BR.A.
1-2-3-4-5
P.F.B.
OES.

FIG. 11

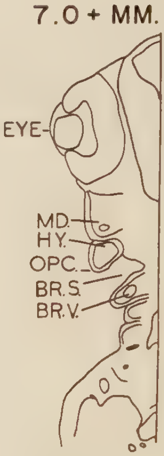
7.0 + MM.
EYE
MD.
HY.
OPC.
BR.S.
BR.V.

FIG. 12

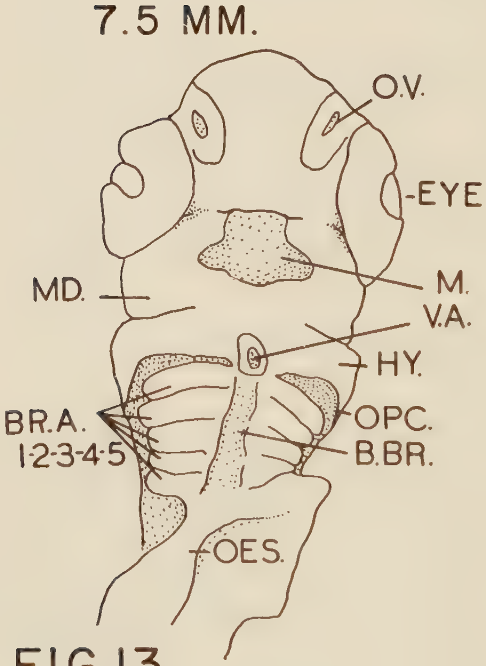
7.5 MM.
O.V.
EYE
MD.
M.
V.A.
HY.
BR.A.
1-2-3-4-5
OPC.
B.BR.
OES.

FIG. 13

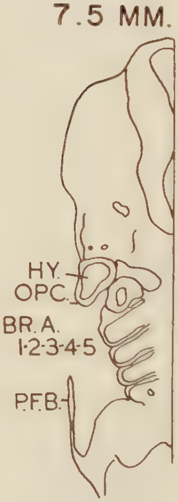
7.5 MM.
HY.
OPC.
BR.A.
1-2-3-4-5
P.F.B.

FIG. 14

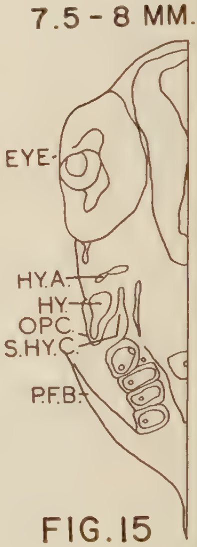
7.5 - 8 MM.
EYE
HY.A.
HY.
OPC.
S.HY.C.
P.F.B.

FIG. 15

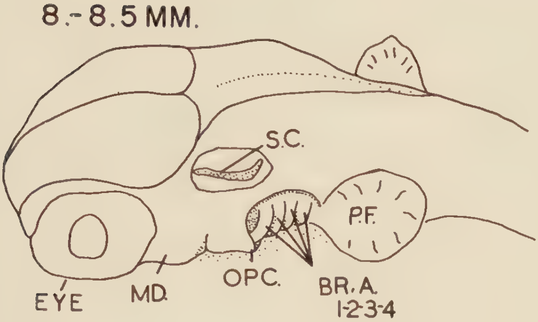

FIG. 16

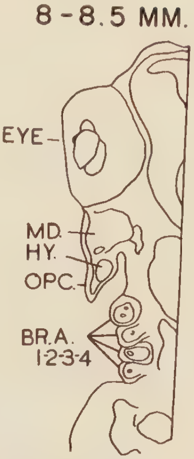

FIG. 17

FIGURES 10–17

Camera lucida and microprojections of embryo trout, whole mounts and coronal sections

FIG. 10. Coronal section through the upper pharyngeal region of a 6.5–7.0 mm embryo showing the opercular fold.

FIG. 11. Ventral aspect of a 7.0 mm embryo dissected from yolk.

FIG. 12. Coronal section through the pharyngeal region of a 7.0 mm embryo showing opercular fold.

FIG. 13. Ventral aspect of a 7.5 mm embryo dissected from yolk and showing mouth opening formed and the opercular fold.

FIG. 14. Coronal section through the pharyngeal region of a 7.5 mm embryo showing the opercular bulge on the hyoid.

FIG. 15. Coronal section through the pharyngeal region of a 7.5 mm embryo showing opercular bulge and the sub-hyoidean chamber.

FIG. 16. Lateral aspect of an 8.0–8.5 mm embryo showing the opercular fold extending caudad.

FIG. 17. Coronal section through the pharyngeal region of an 8.0–8.5 mm embryo showing differentiation in the hyoid.

Abbreviations. — B.BR., basibranchial region of the pharynx; BR.S., first branchial slit between the hyoid and first branchial arch; BR.V., branchial blood vessel; HY., concentration of mesenchyme to become hyomandibular cartilage; HY.A., hyoidean artery; M., mouth; OES., oesophagus; S.C., semicircular canal of auditory vesicle; S.HY.C., sub-hyoidean chamber; V.A., cut end of ventral aorta.

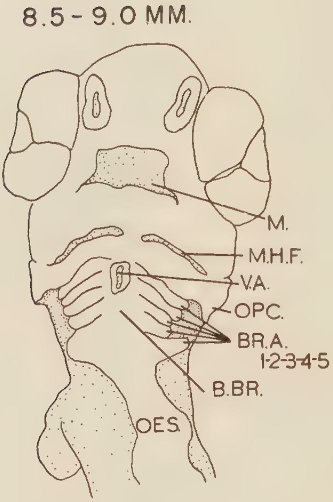
8.5 - 9.0 MM.
M.
M.H.F.
V.A.
OPC.
BR.A.
1-2-3-4-5
B.BR.
OES.

FIG. 18

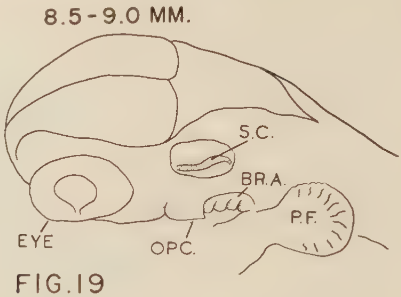
8.5 - 9.0 MM.
S.C.
BR.A.
P.F.
EYE
OPC.

FIG. 19

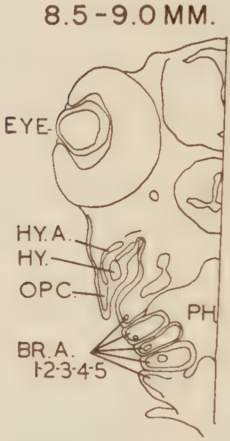
8.5 - 9.0 MM.
EYE
HY.A.
HY.
OPC.
PH
BR.A.
1-2-3-4-5

FIG. 20

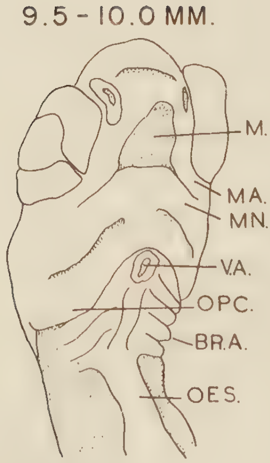
9.5 - 10.0 MM.
M.
MA.
MN.
V.A.
OPC.
BR.A.
OES.

FIG. 21

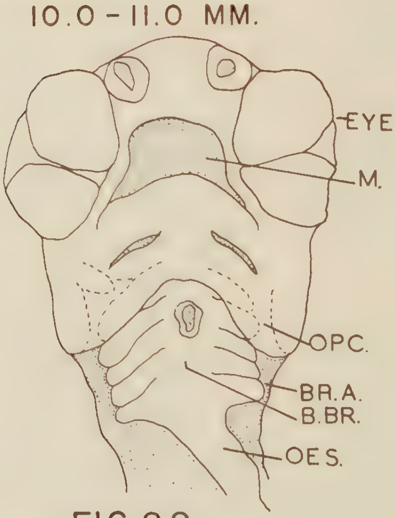
10.0 - 11.0 MM.
EYE
M.
OPC.
BR.A.
B.BR.
OES.

FIG. 22

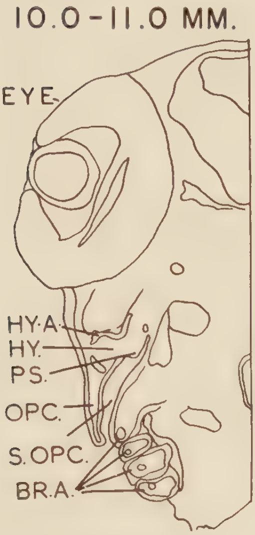

FIG. 23

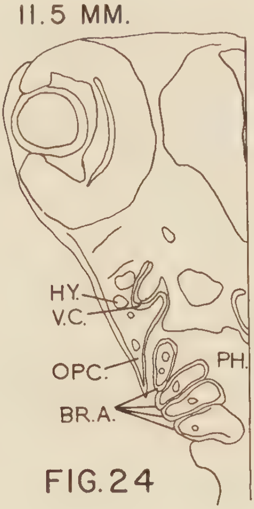

FIG. 24

FIGURES 18–24

Camera lucida and microprojections of embryo trout, whole mounts and coronal sections

FIG. 18. Ventral aspect of an 8.5–9.0 mm embryo dissected from yolk and showing broadening of head and extension of opercular fold.

FIG. 19. Lateral aspect of an 8.5–9.0 mm embryo.

FIG. 20. Coronal section through pharyngeal region of an 8.5–9.0 mm embryo.

FIG. 21. Latero-ventral aspect of a 9.5–10.0 mm embryo dissected from yolk to show the anterior shifting of the mid-ventral region of the mandibular, hyoid and branchial arches.

FIG. 22. Ventral aspect of a 10.0–11.0 mm embryo dissected from yolk.

FIG. 23. Coronal section through the pharyngeal region of a 10.0–11.0 mm embryo.

FIG. 24. Coronal section through the pharyngeal region of an 11.5 mm embryo.

Abbreviations. — HY., hyomandibular precartilage; MA., maxilla; M.H.F., fold between the mandibular and hyoid arches; MN., mandible; PH., lumen of pharynx; PS., developing pseudobranch; S.OPC., subopercular chamber; V.C., cleft between mandibular and hyoid arches.

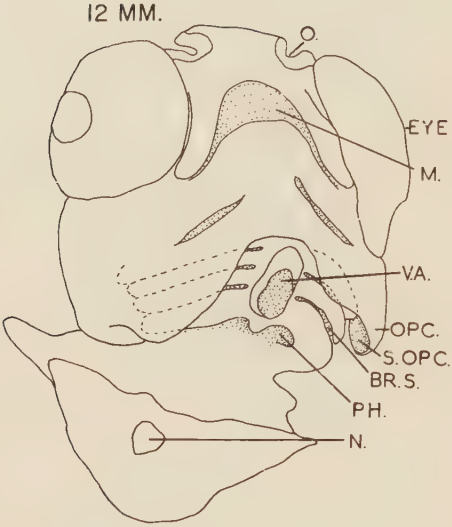
12 MM.
O.
EYE
M.
VA.
OPC.
S. OPC.
BR. S.
PH.
N.

FIG. 25

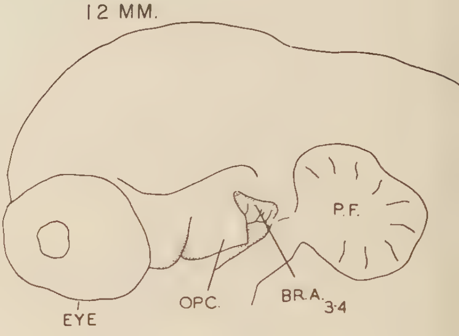
12 MM.
P.F.
EYE
OPC.
BR.A.3-4

FIG. 26

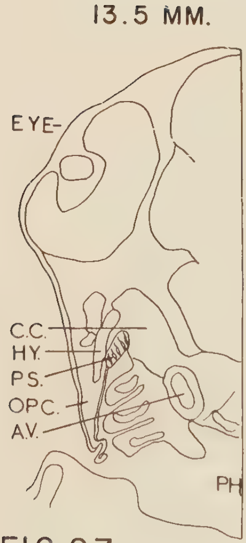
13.5 MM.
EYE
C.C.
HY.
P.S.
OPC.
A.V.
PH

FIG. 27

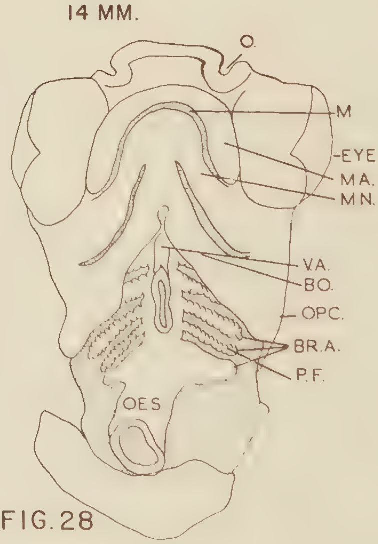
14 MM.
O.
M
EYE
MA.
MN.
VA.
BO.
OPC.
BR.A.
P.F.
OES

FIG. 28

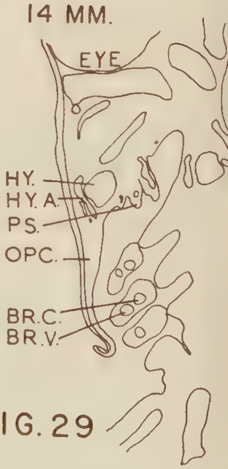
14 MM.
EYE
HY.
HY. A.
P.S.
OPC.
BR.C.
BR.V.

FIG. 29

FIGURES 25–29

Camera lucida and microprojections of embryo trout, whole mounts and coronal sections

FIG. 25. Latero-ventral aspect of a 12.0 mm embryo removed from yolk and showing extent of mouth closure and operculum.

FIG. 26. Lateral aspect of a 12.0 mm embryo showing backward extent of the operculum.

FIG. 27. Coronal section through the pharyngeal region of a 13.5 mm embryo to show complete branchial coverage.

FIG. 28. Lateral aspect of a 14.0 mm embryo removed from the yolk and showing the mouth almost closed, primary filaments on the branchial arches 1 to 4 and the extent of the operculum.

FIG. 29. Coronal section through the pharyngeal region of a 14.0 mm alevin to show internal structure at the time of hatching.

Abbreviations. — A.V., auditory organ; BO., branchiostegal portion of the opercular apparatus; BR.C., branchial cartilage; BR.S., branchial slit; C.C., cranial cartilage; HY., hyomandibular cartilage; N., notochord; O., olfactory organ; OPC., operculum; P.F., primary filaments of the branchial arches; PS., pseudobranch.

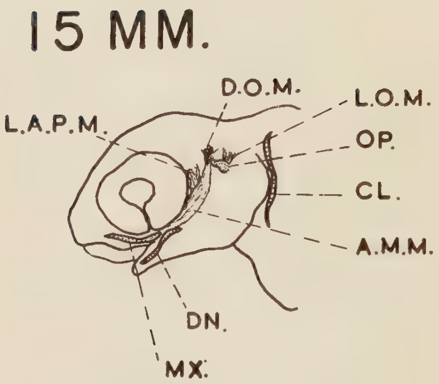
15 MM.
D.O.M.
L.O.M.
L.A.P.M.
OP.
CL.
A.M.M.
DN.
MX.

FIG. 30

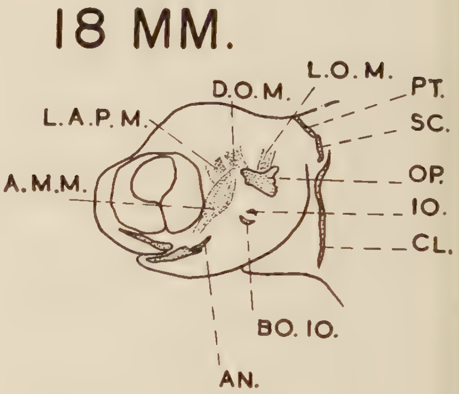
18 MM.
L.O.M.
D.O.M.
PT.
L.A.P.M.
SC.
A.M.M.
OP.
IO.
CL.
BO. IO.
AN.

FIG. 31

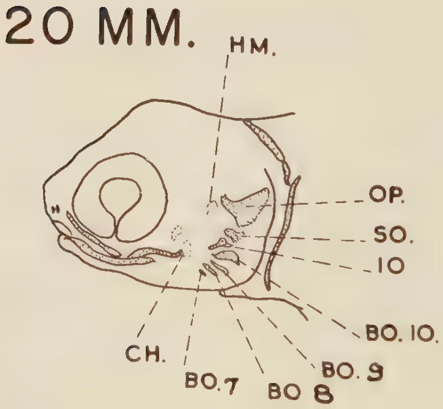
20 MM.
HM.
OP.
SO.
IO
BO. IO.
CH.
BO.7
BO 8
BO. 9

FIG. 33

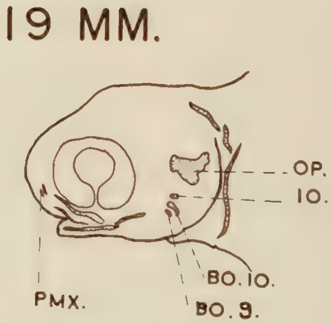
19 MM.
OP.
IO.
BO. IO.
PMX.
BO. 9.

FIG. 32

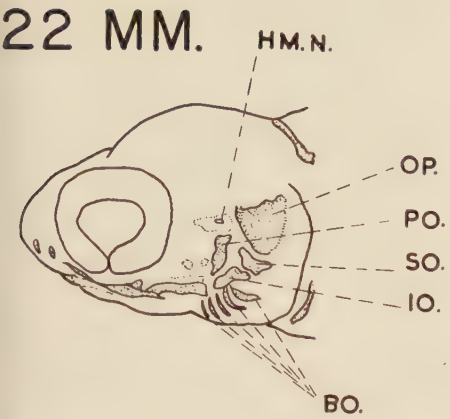

FIG. 34

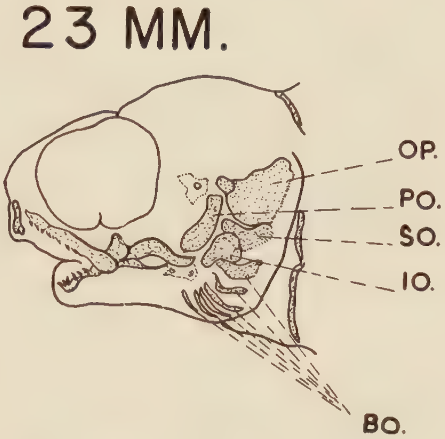

FIG. 35

FIGURES 30–35

Reproduction of cleared and stained alevins and fish of *Salvelinus fontinalis* to show areas of ossification and muscular development in the hyoid and opercular apparatus

Fig. 30. 15 mm alevin.

Fig. 31. 18 mm alevin.

Fig. 32. 19 mm alevin.

Fig. 33. 20 mm alevin.

Fig. 34. 22 mm alevin.

Fig. 35. 23 mm fish.

Abbreviations. — A.M.M., adductor mandibulae muscle; AN., articulare bone; BO., branchiostegal rays; CH., ceratohyal bone; CL., cleithral bone of the pectoral girdle; DH, dentary bone; D.O.M., dilitator operculi muscle; HM., hyomandibular bone; HM.N., foramen for hyomandibular branch of the facial nerve; IO., interopercular; L.A.P.M., levator arcus palatini muscle; L.O.M., levator operculi muscle; MX., maxillary bone; OP., opercular; PMX., premaxillary bone; SC., supracleithrum bone; SO., subopercular.

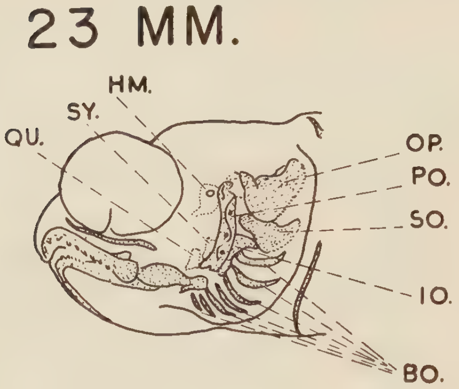
23 MM.
HM.
SY.
QU.
OP.
PO.
SO.
IO.
BO.

FIG. 36

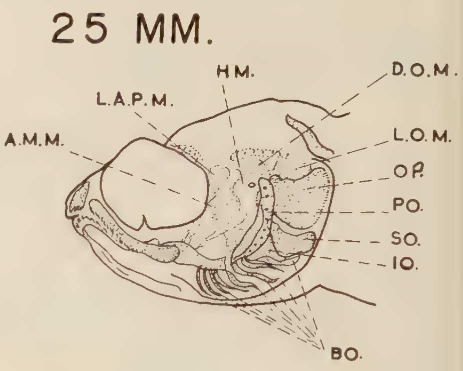
25 MM.
HM.
D.O.M.
L.A.P.M.
A.M.M.
L.O.M.
OP.
PO.
SO.
IO.
BO.

FIG. 37

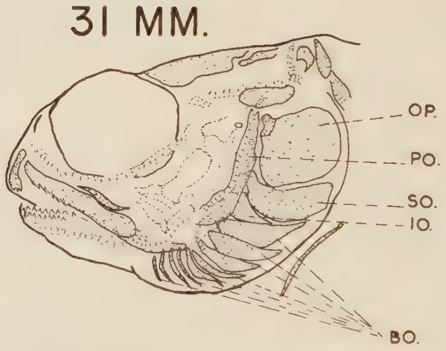
31 MM.
OP.
PO.
SO.
IO.
BO.

FIG. 38

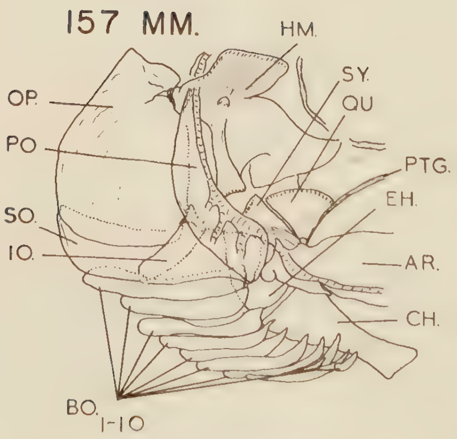
157 MM.
HM.
SY.
QU
OP.
PO
PTG.
EH.
SO.
IO.
AR.
CH.
BO. 1-10

FIG. 39

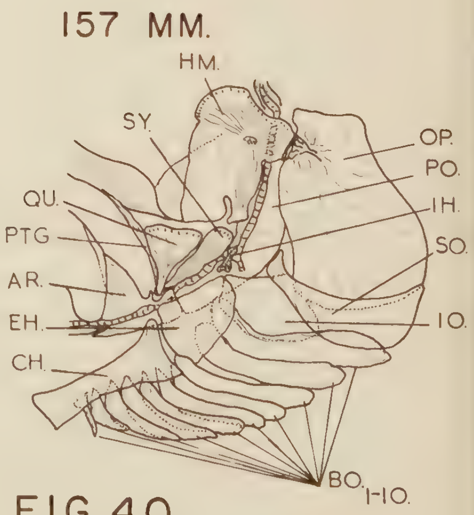
157 MM.
HM.
SY.
OP.
PO.
QU.
IH.
PTG
SO.
AR.
IO.
EH.
CH.
BO. 1-10

FIG. 40

FIGURES 36–40

Reproductions of cleared and alizarin red stained fish of *Salvelinus fontinalis* to show areas of ossification and muscular development in the hyoid arch and opercular apparatus

FIG. 36. 23 mm fish.

FIG. 37. 25 mm fish.

FIG. 38. 31 mm fish.

FIG. 39. 157 mm fish.

FIG. 40. 157 mm fish.

Abbreviations. — AR., articular bone; EH., epihyal bone; IH., interhya bone; PTG., pterygoid; QU., quadrate bone; SY., symplectic bone.

layers at its posterior lateral extremity. The epithelium of the medial surface is one layer in thickness. Scattered goblet cells occur in the epithelium.

5. Following hatching at 14–30 mm length the skeletal elements of the opercular apparatus are developed. Ossification which has appeared in the opercular increases and then commences, successively in the interopercular, the tenth branchiostegal, the ninth branchiostegal, the subopercular, the eighth branchiostegal, the seventh branchiostegal, the preopercular, the sixth branchiostegal and subsequently in the fifth to first branchiostegals.

The musculature of the operculum proper consisting of the levator, dilatator and adductor operculi muscles is complete just at hatching.

ACKNOWLEDGMENTS

To Dr Helen I. Battle, Professor of Zoology, University of Western Ontario, London, for kindly advice and careful supervision, and to the Fisheries Research Board of Canada, and the Department of Fisheries of Canada for specimens, the author is deeply grateful.

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Respiration of the Atlantic Cod[1]

BY RICHARD L. SAUNDERS

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

Measurements of routine and standard rates of oxygen consumption of various sized cod at emperatures between 3 and 15°C revealed a well-marked size effect; small cod consume oxygen t a greater rate per unit weight than do large ones. Increases in temperature raise oxygen con-umption in starved and fed fish. The increase in rate of oxygen consumption of starved fish etween 3 and 10° is proportionately greater than that between 10 and 15°C. Feeding of cod hich have previously been starved increases the rate of oxygen consumption by 40–90%. The ate subsides to the starvation level in 4–7 days depending on temperature and amount of food aten. Handling cod causes them to increase their rate of oxygen consumption; rates return to ormal levels in 3-5 hours. Crowding reduces the rate of oxygen consumption apparently by educing the space for movement and thus restricting activity. Reducing the ambient oxygen from bout 10 to 3 mg/l lowers the rate of oxygen consumption slightly, but the respiratory volume volume of water pumped over the gills per unit time) is markedly increased. This suggests there added stress because the increased metabolic cost of irrigating the gills is not met by increased ates of oxygen consumption.

INTRODUCTION

N IMPORTANT CONSIDERATION in transporting and storing live fish is the equirement for oxygen. Sundnes (1957a, b), in the only published work on od respiration, studied problems involved in transporting live cod and coalfish n well-boats. He determined rates of oxygen consumption of these fishes s affected by size, ambient level of oxygen and the excitement caused by andling. The purpose of the present study was to measure rates of oxygen onsumption of an extensive size range of cod in relation to temperature, crowding, eeding and handling.

MATERIALS AND METHODS

ROCUREMENT AND CARE OF FISH

Cod (*Gadus morhua* Linnaeus) were captured in or near Passamaquoddy ay either by otter trawl or by hook and line. They were kept in large fibreglass anks which were provided with ample volumes of flowing seawater. Aeration as maintained in the holding tanks as a precaution against supersaturation ith atmospheric gases. Cod were fed fresh and frozen herring which they egan to accept after about two weeks in the holding tanks. A minimum time f two months was allowed for cod to become adjusted to laboratory conditions efore using them for experiments. Obviously injured or unhealthy fish were iscarded during this period.

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[1]Received for publication July 18, 1962.

. FISH. RES. BD. CANADA, **20**(2), 1963.
rinted in Canada.

THERMAL ACCLIMATION

Healthy individuals were acclimated in groups of 2 to 12 for minimum periods of 10 days at temperatures of 3, 5, 10 and 15°C. Experiments at 3° were conducted during the winter when the temperature of the water supply was between 0 and 2.5°, and those at 15° during the summer when the temperature of the water supply approached 15°C. Thus, the fish were not subjected to changes in temperature of more than 2–3°C when moved from holding to acclimation tanks.

EXPERIMENTAL PROCEDURES

Measurements of oxygen consumption were made mainly in a mass respirometer which accommodated from 1 to 12 fish depending on their size. This respirometer was a cylindrical fibreglass tank, three feet in diameter and two feet high. It was provided with a floating plywood lid to reduce exchange of atmospheric gases at the surface. Three plexiglass ports in the lid made it possible to observe the fish. The surface of the lid in contact with the water was made convex to facilitate placing it on the water without entrapping air bubbles. Blank experiments demonstrated that the lid was effective in making gaseous exchange negligible. Water entered the respirometer at one side and the rate of flow was measured as it left the other side. Circulation and mixing within the chamber were ensured by means of a submersible pump, held in a water-tight box outside the respirometer, which drew water from one side of the respirometer and returned it to the other side.

Fish were placed in the respirometer at least one day before observations began. The rate of flow through the chamber was adjusted so that the metabolism of the fish did not reduce the ambient oxygen level below about 80% of the air-saturation level.

During an experiment, seawater was passed through the respirometer at a constant rate. Oxygen levels of the ambient water and of that being supplied to the respirometer were measured at intervals. Dissolved oxygen was determined by the sodium azide modification of the Winkler method (American Public Health Association, 1955). The difference in oxygen levels between ambient water and that supplied to the respirometer together with the rate of flow through the respirometer and the combined weight of the fish are used to calculate the rate of oxygen consumption per unit weight of fish. A minimum period of one hour during which the difference between oxygen levels remained nearly constant was chosen as a basis for calculations. The rate of oxygen consumption was determined for the same group of fish on successive days, during which the fish were starved, until it was reasonably stable (within a range of approximately ± 3 mg/kg/hr). This represents the routine level [reflecting "... minor changes in routine physical activity" (Fry, 1957)] for starved fish. After the routine level had been established, the plywood lid was carefully removed and the fish were fed fresh or frozen herring in the respirometer. The lid was replaced and the fish were left undisturbed for an hour after which any uneaten food was removed with as little disturbance as possible. The rate of oxygen consumption always increased following feeding and a maximum was reached from 12–24 hours later.

In some experiments rates of oxygen consumption were measured through two cycles of starving and feeding to see if the minimum and maximum rates could be replicated. Such experiments lasted from 10 days to 2 weeks depending on temperature and the size and number of fish used.

To study the effects of handling, fish were lifted from the respirometer by a dip net and placed in an adjacent tank. After several minutes they were returned to the respirometer and measurements of oxygen consumption were made until the rate returned to the previously established routine level.

Another variant of the experiment was to determine effects of crowding by measuring the rate of oxygen consumption of a group of cod and then repeating the measurements with the remainder after a number of these fish (from one third to one half) had been removed from the respirometer. Measurements were made of routine rates of starved and fed fish before and after the number of fish was reduced. Each of these experiments to determine effects of crowding took about two weeks.

Fish in the mass respirometer were able to swim about to a limited extent. Although some fishes would rest quietly on the bottom of such a respirometer, cod do not. They were observed swimming off the bottom at most times. The freedom of movement in this respirometer is dependent on the degree of crowding and the relation between fish length and diameter of the tank. No analysis was made of the effect on rate of oxygen consumption of the freedom of movement among fish of different lengths.

Since this work was aimed at learning facts about oxygen consumption which might be of value in the practice of transporting or holding live cod, the mass respirometer was an appropriate apparatus to use because conditions of mass holding or transport could be simulated in it. However, it was of interest to gather additional data on the oxygen consumption of single fish under more carefully controlled conditions than were possible in the mass respirometer in order to be able to make comparisons between cod and other species. To this end, a respirometer for single fish was used to measure standard rates by the methods of Saunders (1962). This respirometer holds a fish so that it can breathe without restraint but it does not allow sufficient room for the fish to swim.

RESULTS AND DISCUSSION

The principal results with the mass respirometer including routine rates of oxygen consumption and effects of size, feeding and crowding are summarized in Table I and Fig. 1.

Effects of Size

There is a well-marked effect of size on rate of oxygen consumption. This is shown in Table I where the data are arranged in order of fish size to emphasize that small individuals consume oxygen at a greater rate per unit weight than do large ones. This effect of size is illustrated in Fig. 1. Note that slopes

TABLE I. Routine rates of oxygen consumption of various numbers of starved and fed cod of various sizes and at different temperatures in mass respirometer.

Temperature (°C)	Number of fish	Average size of fish	Range in size of fish	Routine rate of oxygen consumption starved	fed
		kg	*kg*	*mg/kg/hr*	
3	7	0.43	0.22 – 0.58	50	73
3	7 *	1.04	0.81 – 1.20	38	–
3	4	1.12	1.04 – 1.20	44	–
3	5 *	1.64	1.28 – 1.95	40	–
3	3	1.45	1.28 – 1.70	43	–
3	3	2.81	2.69 – 2.88	36	–
3	1	6.65	. . .	28	–
10	8	0.32	0.19 – 0.39	74	116
10	6	0.64	0.52 – 0.83	67	105
10	6 *	1.07	0.84 – 1.27	72	113
10	4	1.00	0.84 – 1.12	73	111
10	4	1.98	1.52 – 2.39	63	–
10	4	2.96	2.48 – 3.23	66	85
10	1	7.10	. . .	50	70
15	8	0.15	0.09 – 0.20	153	229
15	8	0.43	0.34 – 0.52	92	136
15	5 *	0.46	0.34 – 0.57	78	150
15	3	0.49	0.34 – 0.57	88	156
15	6 *	1.42	1.12 – 1.74	72	103
15	4	1.34	1.12 – 1.49	89	126
15	4	1.65	1.40 – 2.29	70	107
15	2	3.05	2.96 – 3.14	61	92

*The lines of data so indicated are results of experiments illustrating the effects of crowding on the rate of oxygen consumption. Experiments were conducted first with the number of individuals indicated in the first line of each pair and then with the reduced numbers indicated in the second line.

always have values less than 1.0 showing that small fish use more oxygen per unit weight than do large ones. During the experiments at 15°C some unusually small cod were available for study. Their weights ranged from 90 to 200 g (average, 150 g). Their rates of oxygen consumption per unit weight were much greater than those of slightly larger fish as shown in Table I. In Fig. 1c, the rates for these small fish are substantially higher than the established trend for larger fish.

A limited series of measurements of oxygen consumption was made with the single-fish respirometer to establish by comparison to what extent the slight amount of swimming in the mass respirometer increased the rate of oxygen consumption over that measured for non-swimming fish (Table II, Fig. 1). Saunders (1962) demonstrated that rates of oxygen consumption measured in a single-fish respirometer under quiet conditions in air-saturated water were essentially the standard rates of oxygen consumption of two out of the three freshwater species studied. In the absence of more precise data, those obtained using the single-fish respirometer are considered as standard rates of oxygen consumption as described by Fry (1947). Further support for the assumption

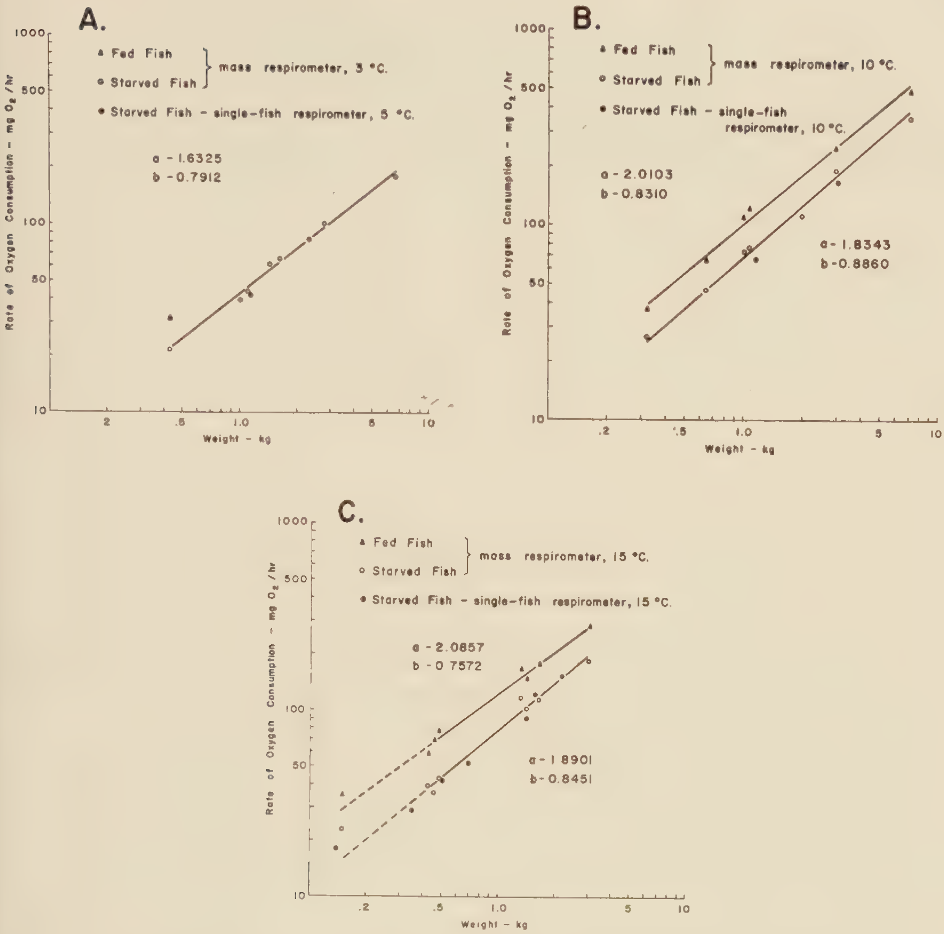

FIG. 1. Relations between size of fish and routine rate of oxygen consumption at various temperatures among starved and recently fed individuals. Lines of best fit have been calculated by the method of least squares for the data obtained using the mass respirometer. The values in Panel C for the fish weighing 0.15 kg were not included in these calculations. Data from individuals in the single-fish respirometer are given for comparison. Note in Panel A that mass experiments were conducted at 3°C and experiments with single fish at 5°C. The "a" (intercept) and "b" (slope) values for regression lines are indicated.

that the data of Table II represent standard rates is the observation that the cod rested quietly in the respirometer during experiments. The rates from experiments with the single-fish respirometer are, in general, slightly lower than those from experiments with starved fish in the mass respirometer (Fig. 1) and this suggests that the latter are slightly higher than standard rates.

Sundnes (1957a, b) gives values of 51 and 73 mg O_2/kg/hr for resting cod weighing 1.75 kg and 0.28 kg respectively at temperatures varying between

TABLE II. Standard rates of oxygen consumption of starved cod of various sizes and at different temperatures in single-fish respirometer.

Temperature (°C)	Size of fish	Rate of oxygen consumption
	kg	*mg/kg/hr*
5	1.14	39
5	2.33	36
10	1.15	58
10	3.03	55
15	0.14	130
15	0.35	84
15	0.51	82
15	0.70	75
15	1.44	63
15	1.58	78
15	2.20	71

8.7 and 10.7°C. These are roughly comparable with the routine rates at 10°C of 64 and 80 mg/kg/hr which were obtained by interpolation from Fig. 1b for fish weighing the same as those used by Sundnes.

The slopes of the straight lines expressed in Fig. 1 vary between 0.76 and 0.89. Fry (1957) described the relationship between rate of oxygen consumption and weight for a number of species. The slopes of the lines described by Fry are of the order of 0.8. Similarly, Winberg (1956, 1961) in an extensive review of the literature found that the rate of oxygen consumption of many fishes, both freshwater and marine, is proportional to the fish weight raised to a power of about 0.8. In the present work the slopes of the lines relating routine rate of oxygen consumption to weight in starved fish vary between 0.79 and 0.89 and those for fed fish between 0.76 and 0.83 (Fig. 1).

EFFECTS OF TEMPERATURE

The effects of temperature on the routine rate of oxygen consumption are summarized in Tables I and III, and illustrated in Fig. 1 and 2. Fig. 1 shows that the increase in rate of oxygen consumption of starved fish between 3 and 10° is proportionately greater than that between 10 and 15°C. The data from Table III are presented graphically in Fig. 2. The difference between the curves for fish of different weights is demonstrated by multiplying the rates of 6 kg fish by an appropriate constant factor (0.129) to reduce them to the general level of those for 0.5 kg fish. The resulting values are shown by open circles. Fig. 2 shows that the rate of oxygen consumption increases more in large than in small fish as temperature is increased from 3 to 10° and that between 10 and 15° the rate levels off in large cod but continues to rise in small ones.

TABLE III. Routine rates of oxygen consumption of various sized, starved cod thermally acclimated at three temperatures. These values were calculated from the regression lines of Fig. 1. Rates of oxygen consumption are given in mg/hr.

Size (kg)	Temperature (°C)		
	3	10	15
.5	25	37	46
1.0	43	68	78
3.0	102	182	197
6.0	178	334	354*

*The value for 6 kg fish at 15°C was obtained by extrapolation.

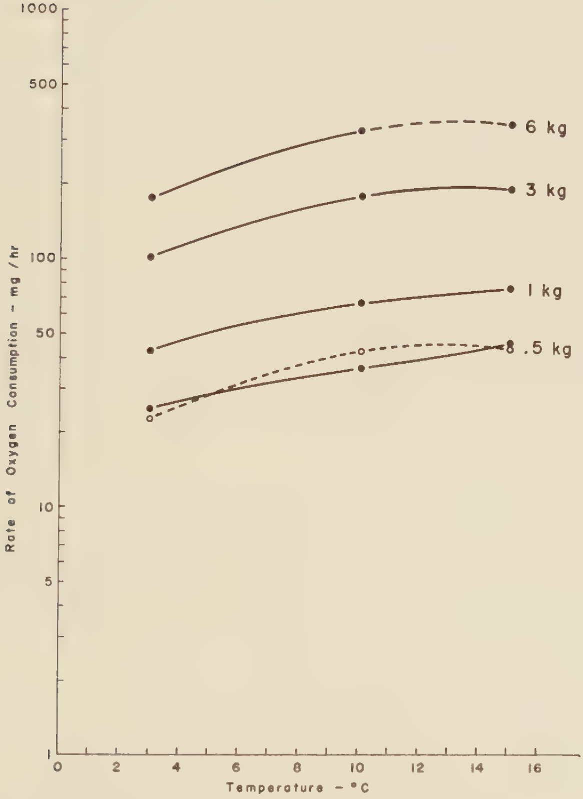

FIG. 2. Relation between rate of oxygen consumption and temperature in thermally acclimated, starved cod of different sizes. The open circles represent the values for 6 kg fish multiplied by a factor of 0.129 to reduce them for comparison to the general level of the points for 0.5 kg fish. The value for 6 kg fish at 15°C was obtained by extrapolation. Numerical data are given in Table III.

EFFECTS OF FEEDING

Rates of oxygen consumption increased by as much as 95% when starved cod were given an abundance of herring and left undisturbed for about 2 hours (Table I, Fig. 1b and 1c). Generally, increases in rates of oxygen consumption amounted to no more than 40–60%. In the species for which active and standard rates have been measured, active rates of oxygen consumption are more than twice the standard rates (Fry, 1957; Basu, 1959). Although Job (1954) found that feeding brook trout (*Salvelinus fontinalis*) to satiety had the effect of raising the rate of oxygen consumption to the active rate, it is unlikely that the rates of fed cod reached the active levels.

Figure 3 illustrates the duration of increased rates of oxygen consumption at 10°C following feeding of six cod (average weight 1.07 kg). These took about 7 days to return to the previously established starvation level. Another group of four fish at 10°C (average weight 1.0 kg) also took 7 days to return to the starvation level following feeding. At 15° groups of various numbers and with average weight between 0.5 and 1.7 kg took only 4 to 5 days to return to the starvation level. At this same temperature, two large fish (average weight 3.1 kg) took 8 days to return to the starvation rate. The duration of elevated rates of oxygen consumption following feeding is probably governed by temperature and the amount of food eaten, although this is not brought out clearly in the present study.

It is interesting that at a temperature of 3°C only the smallest cod would eat even after being starved as long as 2 weeks. Since the small fish were not mature, but many of the fish weighing 1 kg and more were observed to be mature (ripe) and sometimes spawning (during February and March when experiments at 3°C were done), it is suggested that mature cod do not feed. These observations are at variance with those of Marcotte (1961) and Jean (personal com-

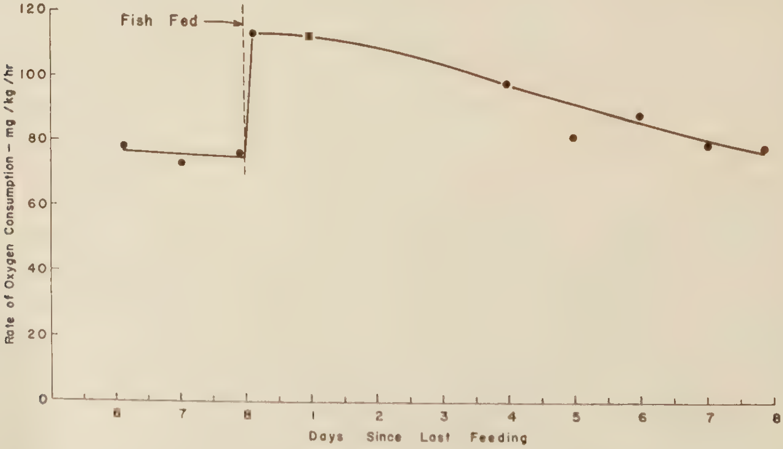

FIG. 3. Duration of the increased rate of oxygen consumption brought about by feeding. Data are from a series of experiments at 10°C with 6 fish of average weight 1.07 kg (range 0.84–1.27 kg) in mass respirometer.

munication) that differences in volume of stomach contents between mature and immature cod are slight. Moreover, Jean's mature, feeding cod were captured in water as cold as 0°C. McKenzie (1935) reported that cod feed sparingly at temperatures of about 1°C and but rarely at 0°C. He reports that in very cold water the smallest cod eat more frequently and at slightly lower temperatures than the larger ones. However, Kohler (1961) demonstrated that cod do feed at temperatures as low as 2°C but at a reduced rate as compared with that at 10 or 12°C.

EFFECTS OF HANDLING

It has been demonstrated by Sundnes (1957b) that handling of cod and pollock raises their rates of oxygen consumption considerably above the previously established routine level. Sundnes considered this phenomenon in connection with the commercial practice in Norway of carrying live cod and pollock in well-boats. He found that rates of oxygen consumption of small individuals (*ca.* 0.25 kg) of both species take somewhat less than one day to return to previously established routine levels following handling, but those of large ones (>1.0 kg) take about three days. In the present study, rates of oxygen consumption of starved cod increased by as much as 70% following handling and returned to routine levels in as little as 3 to 5 hours in various numbers of cod with average weights between 0.4 and 2.8 kg. These experiments were done at 3°C, whereas those reported by Sundnes were at temperatures between 8.7 and 10.7°C. On the basis of present findings concerning the duration of increased rates of oxygen consumption following handling, it is suggested that rates of oxygen consumption of Sundnes' large fish, which had been unfed for only 3 to 4 days prior to being handled, may not have been starved long enough to be at starvation levels prior to experiments.

EFFECTS OF CROWDING

It is established in this study that rates of oxygen consumption per unit weight of fish are influenced by the number of fish present in the mass respirometer. The effect of crowding is to decrease the rate of oxygen consumption (Table 1, Fig. 4). Although the effects of reducing numbers of individuals in the respirometer were small in some cases, there were increased rates of oxygen consumption in seven out of eight tests. In two experiments at 3°C there were noticeable rises in rates of oxygen consumption when the number of fish was reduced. In a single experiment at 10°C, the rates of oxygen consumption of starved and fed cod remained essentially the same when the number of fish was reduced from six to four. In two experiments at 15°C there were marked increases in rates of oxygen consumption of both starved and fed cod when numbers of individuals in the respirometer were reduced.

It is suggested that crowding reduces the rate of oxygen consumption by restricting the activity of the fish. A few cod in the respirometer have more room to swim around and consequently consume oxygen at a higher rate than greater numbers of similar sized cod in the same space. It is significant that Horton (1956) reported lower rates of postplanting mortality when rainbow

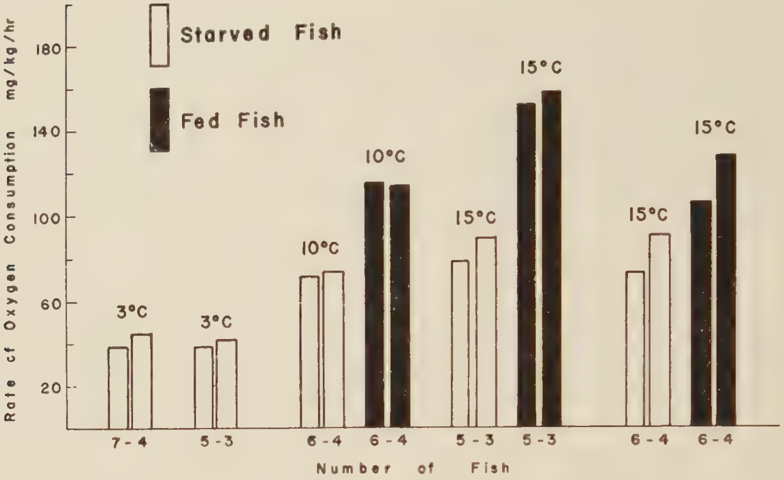

FIG. 4. Effect of degree of crowding on routine rate of oxygen consumption. Measurements were made first for the number of fish indicated below the left of each pair of bars. A number of fish were removed from the respirometer and the measurements repeated for the fish remaining (number indicated below right bar of each pair). The experiments at 10 and 15°C were carried through two cycles of starvation and feeding. Rates of starved and fed fish were determined in the first cycle for the greatest number of fish and the cycle was repeated after a number of fish had been removed from the respirometer.

trout (*Salmo gairdneri*) were transported under crowded conditions than under less crowded conditions. Since it is desirable to reduce activity metabolism among fish being transported (Norris *et al.*, 1960), and this may be accomplished by lowering the temperature or by using drugs, crowding within certain limits may have the same beneficial effects as reducing temperature or using drugs.

EFFECTS OF REDUCED OXYGEN LEVELS

Since it may not always be possible to maintain ambient oxygen levels above 80% of the air-saturation level, it is important to consider what may happen to rates of oxygen consumption when ambient oxygen is reduced. Data were obtained from two sets of experiments with the single-fish respirometer. Fig. 5 indicates that the resting rate of oxygen consumption is little changed, but that respiratory volume (the volume of water pumped over the gills per unit time) increases markedly as the ambient oxygen level decreases from 10 to 3 mg O_2/l. In the smaller individual oxygen consumption decreased from 40 to 30 mg/kg/hr as ambient oxygen was reduced from 9.5 to 3 mg/l. In the larger individual there was no change in oxygen consumption over this range of ambient oxygen. In the smaller fish the increase in respiratory volume over the decreasing oxygen range is from 7.1 to 27.1 l/hr while that of the large fish is from 18 to 90 l/hr. Although the rate of oxygen consumption changes little over this range of ambient oxygen, it is significant that respiratory volumes increase. Saunders (1962)

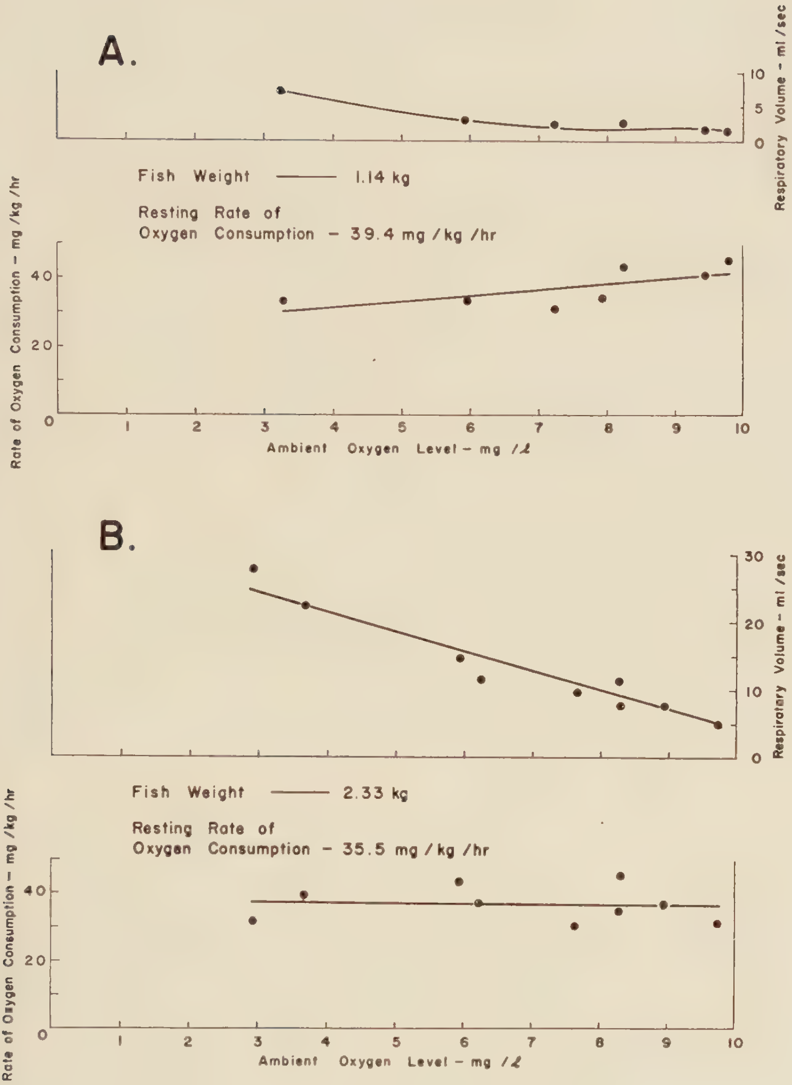

FIG. 5. Effects of changing ambient oxygen levels on rates of oxygen consumption and respiratory volumes. The rates of oxygen consumption and respiratory volumes were determined at various ambient oxygen levels for these two individuals using the single-fish respirometer. Ambient oxygen levels were reduced by steps over a period of 24 hours. Measurements of oxygen consumption and respiratory volume were made during periods when the ambient oxygen level remained relatively constant for 30 minutes or more. Lines for rate of oxygen consumption were fitted to the data by the method of least squares; those for respiratory volume were fitted by inspection. The resting rates indicated were determined in other experiments with these fish in which ambient oxygen levels were held near air saturation.

demonstrated with three freshwater species that reduced ambient oxygen levels always brought about increased respiratory volumes. It is possible that cod may be under increased stress at all levels of oxygen below air saturation because respiratory volumes increase and oxygen consumption does not increase to keep pace with the increased metabolic cost of irrigating the gills. However, cod in nature probably depend to a large extent on swimming to force water over their gills and do not depend on active gill irrigation to the extent that some species do. Thus, gill irrigation might be accomplished as a by-product of swimming and require little expenditure of energy beyond that for swimming.

Owing to the increased metabolic cost of irrigating the gills without an attendant increase in the rate of oxygen consumption, it is possible that cod under conditions of live storage or transport may be unable to live for extended periods at reduced oxygen levels since they would have to rely on anaerobic metabolism for part of their energy requirements. Moreover, the effects of increased activity would probably exaggerate the harmful effects of lowered oxygen levels suggested here for resting fish.

ACKNOWLEDGMENTS

I am grateful to Messrs R. J. Gibson and A. E. Neumeyer who carried out the experiments. Mr F. E. Purton maintained the stock of fish. I appreciate the helpful suggestions given by Drs J. L. Hart, F. D. McCracken and D. W. McLeese during preparation of the manuscript. Special thanks are due to Mr P. W. G. McMullon and Miss Frances Armstrong for preparing the illustrations and typing the manuscript respectively.

SUMMARY

Rates of oxygen consumption of various sized cod were measured under different conditions of temperature and crowding and with starved and recently fed individuals. Some of the measurements of oxygen consumption (routine rates) were made with groups of from one to twelve fish in a mass respirometer while others (standard rates) were made with one fish at a time in a single-fish respirometer. The effects of crowding and handling on routine rates of oxygen consumption were studied. A limited number of experiments were done to study the effect of low ambient levels of oxygen on the standard rate of oxygen consumption of starved fish.

1. Small cod consume oxygen at a greater rate per unit weight than do large ones. The slope of the regression line which relates the logarithm of fish weight to the logarithm of routine rate of oxygen consumption in mg/hr is between 0.79 and 0.89 in starved and between 0.76 and 0.83 in recently fed fish.
2. Rates of oxygen consumption measured in the single-fish respirometer are slightly lower than those measured in the mass respirometer.

An increase in temperature brings about rises in the rates of oxygen consumption of starved and fed cod. There is a greater rise in the rate of oxygen consumption as temperature increases from 3 to 10 than from 10 to 15°C.

The rate of oxygen consumption of starved cod may be increased by from 40 to 90% by feeding them. The duration of this increased rate is from 4 to 7 days. Oxygen consumption of cod at 15° returns to the rate for starved fish more quickly than for those at 10°C.

Handling of cod may result in increasing the rate of oxygen consumption by as much as 70%. These increased rates for starved individuals subside to previously established routine levels in less than one day.

An effect of crowding is to reduce the rate of oxygen consumption per unit weight of fish. It is suggested that crowding reduces the space for movement with the result that fish swim less and demand less oxygen than under conditions wherein they can be more active.

Although the rate of oxygen consumption is reduced slightly or not at all by lowering the ambient oxygen level from 10 to 3 mg/l, the volume of water pumped over the gills (the respiratory volume) is markedly increased. It is suggested that such increased respiratory volumes place stress on the fish because the rate of oxygen consumption does not keep pace with the increased metabolic cost of irrigating the gills.

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Resistance of Four Freshwater Crustaceans to Lethal High Temperature and Low Oxygen[1,2]

BY J. B. SPRAGUE

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

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[1] Received for publication September 5, 1962.

[2] Based upon portions of a thesis accepted by the Faculty of Graduate Studies, University Toronto, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

FISH. RES. BD. CANADA, **20**(2), 1963.
nted in Canada.

ABSTRACT

The crustaceans studied were the isopod *Asellus intermedius* Forbes, and the amphipods *Hyalella azteca* (Saussure), *Gammarus fasciatus* Say, and *Gammarus pseudolimnaeus* Bousfield.

Resistance to high temperature decreased with size in *A. intermedius* and *G. fasciatus*, but no difference was found for *H. azteca*. Female *Gammarus* were more resistant than males, there was no difference for *A. intermedius*, and a variable relation in *H. azteca*. Acclimation temperature could be raised at rates of 2.5 to 5°C per day, at temperatures above 14°C. Raising acclimation from 10 to 20°C increased the lethal temperature (50% mortality in 24 hours) by 1.9°C in *G. fasciatus*, 1.3°C in *A. intermedius*, 0.5°C in *G. pseudolimnaeus*, and apparently not at all in *H. azteca*. There was no seasonal variation in resistance after *A. intermedius* was acclimated in the laboratory.

Two difficulties encountered were mortality during acclimation and short survival of controls, but careful checking showed that neither greatly affected the reported resistance.

Estimates of the ultimate 24-hour lethal temperatures were 34.6°C for *A. intermedius* and *G. fasciatus*, 33.2°C for *H. azteca*, and 29.6°C for *G. pseudolimnaeus*. The concentrations of low oxygen causing 50% mortality in 24 hours, with acclimation and testing at 20°C, were 0.03 mg/l for *A. intermedius*, 0.7 mg/l for *H. azteca*, 2.2 mg/l for *G. pseudolimnaeus*, and 4.3 mg/l for *G. fasciatus*. Lethal temperatures would seldom seem to affect distribution under natural conditions, but resistance to low oxygen fits field observations fairly closely.

INTRODUCTION

A MAJOR PURPOSE of this investigation is to show whether lethal levels of high temperature and low oxygen are important in determining the type of habitat utilized by each of the four crustaceans. The work was stimulated by the usefulness of the larger freshwater invertebrates as biological indicators. Invertebrate indicators are now frequently used in water pollution surveys, and have been used for classifying stream temperatures (Hallam, 1959). Such systems of biological indicators depend on earlier field work correlating distribution of species with levels of temperature (Ide, 1935) or oxygen (Gaufin, 1958) in the environment.

The present investigation was undertaken to extend this knowledge by laboratory study of lethal levels. One species of Isopoda, and three of Amphipoda, were chosen because they were common, and characteristic of habitats which differ in temperature or oxygen content.

Terminology and methods used in this study are mostly those developed by Fry (1947) and his co-workers (Hart, 1952; Brett, 1952; Shepard, 1955). There is less work of this scope on invertebrates, but McLeese (1956) determined the tolerance of the lobster to three interrelated lethal factors, and Baldwin (1954) made a thorough study of lethal temperatures for a terrestrial insect.

Two main difficulties in this investigation are discussed in the section on tolerance of laboratory conditions. There was sometimes heavy mortality during holding, and survival-times were short in some control experiments. Steps were taken to minimize or eliminate any effects on the resistance which is reported.

MATERIALS AND METHODS

SPECIES USED[3]

The isopod studied was *Asellus intermedius* Forbes, sometimes called *A. communis* Say, a synonym (Pennak, 1953). Specimens of this animal, and of ie three amphipods, have been deposited in the Royal Ontario Museum of oology. Field observations show that *A. intermedius* has a broad spectrum ecological requirements (Ellis and Gowing, 1957; Hallam, 1959; Hatchett, 947) but can withstand water which is very warm, or drastically reduced in xygen content (Gaufin and Tarzwell, 1952, 1955; Sprague, 1954).

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[3] A more detailed version of this and other sections of the paper is available in manuscript form (Sprague, 1959). In particular, exact survival-times are listed for all experiments.

Hyalella azteca (Saussure) is the most widely distributed amphipod in North merica. It seems to be as tolerant as *A. intermedius* of high temperatures Bousfield, 1958; Embody, 1912; Hallam, 1959), but not of such severe dexygenation (Gaufin, 1958; Sprague, 1954).

The other two amphipods used in the study were *Gammarus fasciatus* Say nd *G. pseudolimnaeus* Bousfield. *G. fasciatus* is characteristic of waters which re slow and warm (Clemens, 1950; Embody, 1912; Pentland, 1930) while *G. seudolimnaeus* is restricted to cool waters (Bousfield, 1958). Neither species eems to be found in water which suffers more than mild deoxygenation.

OLLECTING AND MAINTAINING ANIMALS

Experimental animals were collected in the field at locations where they ere abundant. *A. intermedius* came from Underwood Creek, in Collingwood, ntario. *H. azteca* and *G. fasciatus* were collected in Frenchman's Bay, on Lake ntario east of Toronto. *G. pseudolimnaeus* was obtained from Silver Creek, t the top of the Niagara escarpment near Collingwood. All species were btained in greatest abundance by sorting them from the vegetation of their abitat by means of large-bore pipettes.

Animals were acclimated at a constant temperature before being used in xperiments. They were maintained by species in 20-litre glazed crocks half lled with dechlorinated tap water and aerated. Each group of crustaceans was iven about two handfuls of vegetation from its own habitat for food. Deposits f refuse on the bottom were siphoned out periodically, and fresh water was dded. The crocks were placed in constant temperature baths maintained ithin 1°C of the desired level. Acclimation in the laboratory proceeded for t least one day for each Centrigrade degree of change from the habitat temperture at the time of collecting. A minimum of 6 days was allowed in all cases, nd the usual maximum was 30 days.

ROCEDURE FOR TESTING

The measure of resistance used in this work was time to 50% mortality at a iven constant level of temperature or dissolved oxygen. An average of 40 ndividuals was used to determine a single time to 50% mortality. These were xposed to the experimental condition for different periods of time in groups of or 10.

Following exposure, the animals were given a recovery period of 12 to 24 ours at a temperature of about 18°C. The criterion of death was inability o locomote in a normal co-ordinated fashion after this waiting period. Usually here was no doubt whether an animal was dead or alive. However in some xperiments using very severe levels of the lethal factor, many individuals showed eak or erratic locomotion 12 hours after exposure, and invariably died within few days.

Resistance varied with weight and sex, parameters which could only be determined after completing an experiment. Therefore, the dead and live animals from each group were preserved separately in 70% alcohol for later determination of weight and sex. Preservation resulted in reported weights about 20% lower than fresh wet weights. The arithmetic mean weight was used to characterize each group of animals which determined a 50% mortality time. Occasional individuals which differed greatly in weight from the rest of the group were excluded from the experiment.

The treatment of results to obtain median survival-time followed the graphical procedure of Litchfield and Wilcoxon (1949). Percentage mortalities in the groups were plotted against exposure times. Lines were fitted by eye to the points on logarithmic-probability paper, as illustrated by the examples in Fig. 1. The goodness of fit was calculated (*loc. cit.*) and often the line was redrawn and tested to obtain the best fit. Results were discarded if the probability value of the line was less than .05. In Fig. 1, the probability values for the lines from 38 to 34°C are .86, .64, .63, .25, and .08. The time to 50% mortality was read from the graph. This parameter is hereafter designated as the LT50, signifying "*lethal time for 50% of the individuals*". The number of animals and a slope factor were then used in nomograms of Litchfield and Wilcoxon (1949) to obtain 95% confidence limits for the LT50. These in turn could be used to determine whether two LT50's were significantly different.

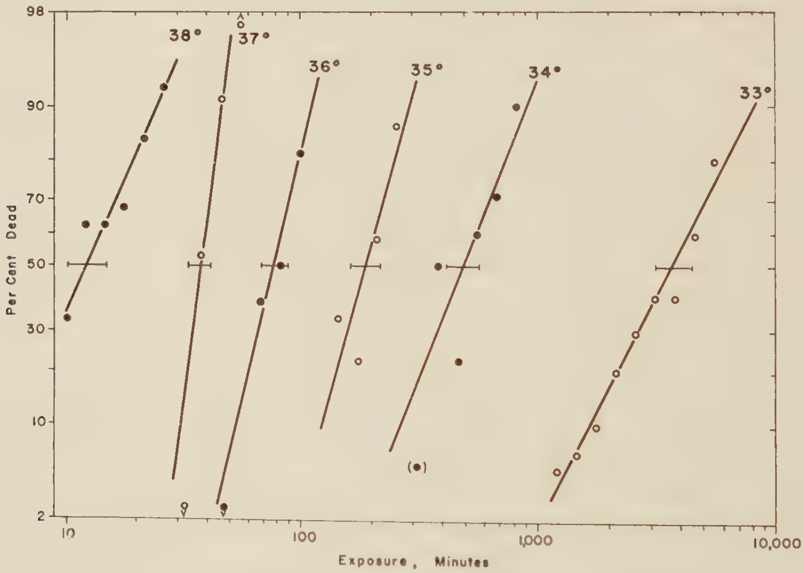

FIG. 1. Mortality of *Asellus intermedius* acclimated at 25°C and tested at various temperatures. Numbers in the body of the graph are experimental temperatures in degrees Centigrade. The 95% confidence limits of each time to 50% mortality are indicated by a horizontal line. A "V" indicates mortality less than 2%, or more than 98%. The bracketed point is corrected from 0% according to the method of Litchfield and Wilcoxon (1949). One week equals 10,080 minutes.

Of the 232 LT50's used in the main part of this work, about 20% involved long exposure times of one or more weeks, and were obtained by slightly different methods. In these experiments, the progress of mortality was followed by successive inspections of the same group of animals. Order of death within a group was not known, and hence no restrictions of weight or sex could be imposed afterwards. Results were analysed by the methods of Litchfield (1949), similar to those described above except that goodness of fit could not be estimated. Such a case is illustrated in Fig. 1 by the experiment at 33°C. All temperatures are stated in degrees Centigrade (Celsius).

Apparatus and Its Performance

For experiments on lethal temperature, animals were suspended in water baths in numbered glass tubes 8 cm long, 4 cm in diameter, and closed with nylon net. The metal baths held 43 litres, and were coated inside with well-aged aluminum paint. Temperatures in the baths were controlled to within ±0.1°. Dissolved oxygen was maintained at or near saturation values by vigorous aeration. Lighting was standardized to some extent by placing a 40-watt electric light one metre above the water bath. Baths were filled one or two days before an experiment with tap water which had passed through activated carbon for chlorine removal. A mineral analysis of the water is given in Table I.

Table I. Mineral analysis* of Toronto tap water for 1953–54.

pH	7.7
Total solids	171 mg/l
Total hardness as $CaCO_3$	132 mg/l
Total alkalinity as $CaCO_3$	91 mg/l
Calcium	39 mg/l
Magnesium	8.5 mg/l
Sodium and potassium (6:1)	7.8 mg/l
Aluminum (Al_2O_3)	0.3 mg/l
Iron (Fe_2O_3)	0.04 mg/l
Sulphate	24 mg/l
Chloride	21 mg/l

*Provided by the Director of Water Purification for Metropolitan Toronto.

Water of reduced oxygen content was obtained by a continous-flow exchange column using nitrogen, similar to that described by Shepard (1955). Dissolved oxygen was determined at the outlets of 250 ml. Erlenmeyer experimental flasks by the Alsterberg modification of the Winkler method (American Public Health Association, 1955). On the average, 10 measurements of dissolved oxygen were made during an experimental run. Excluding experiments below 0.1 mg/l, 90% of the oxygen determinations were within 15% of the mean value. Larger deviations were corrected quickly. An experimental run was characterized by the mean value of determinations, each weighted for time elapsed since the previous one. Temperature measurements were all within 1.5° of the nominal value.

The carbon filter in the oxygen-reducing apparatus did not remove all chlorine from the water. Tests by the orthotolidine method (American Public Health Association, 1955) showed that chlorine residual varied from a trace to 0.04 mg/l, compared to untreated tap water which had up to 0.2 mg/l. The filter would have handled any "surges" of chlorine in the supply water, since it reduced heavy experimental loads to 0.04 mg/l.

EFFECTS OF CERTAIN FACTORS ON RESISTANCE

Tolerance of Laboratory Conditions

During acclimation

One of the difficulties encountered was high mortality of animals during acclimation. Reasonably accurate records of mortality are available for 18 groups of acclimating animals, about one quarter of the total number. Mortalities of *A. intermedius* and *G. pseudolimnaeus* were similar and averaged 28% during 4 weeks of holding.[4] For the other two species, *H. azteca* and *G. fasciatus*, mortality was much higher and averaged 56%.[4]

A probable reason for excessive mortality was cannibalism associated with over crowding. Partly-consumed amphipods were often found, and slightly-injured individuals were frequently seen to be under attack. Deaths of *A. intermedius* were proportionately higher in more crowded acclimation crocks, as shown in Table II. Wilder (1940) had similar findings for mortality of *Hyalella azteca* over a similar range of densities. Sexton (1928) records cannibalism as an important difficulty in rearing European *Gammarus*, while Clemens (1950) mentions the same problem with *G. fasciatus*. Embody (1912) kept *G. fasciatus* and *H. azteca* in the laboratory, and found that individuals were often eaten after they had moulted. Since these animals moult every one to two weeks at 20° (Bovee, 1951; Clemens, 1950), cannibalism after moulting may have accounted for a major portion of the mortality recorded for both species.

Table II. Percentage mortality of *Asellus intermedius* during acclimation as related to degree of crowding.

Acclimation temperature	Initial number of individuals	Mortality during four weeks of holding
20°C	500	3%
"	500	10%
"	1,500	22%
"	3,000	40%
30°C	600	18%
"	1,500	37%

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[4] These figures were obtained by recalculating mortality to a 4-week basis in some of the groups, assuming a constant mortality rate. Since animals were removed from most groups for use in experiments, the natural mortality was distinguished from this "fishing mortality" by the methods of Ricker (1958, pages 24 to 26).

Nevertheless the possibility remains that mortality during acclimation may have been caused by low vitality, which may have influenced resistance in lethal tests. This does not seem to have been the case for *A. intermedius*, since there was no change in heat-resistance during 4 weeks in the laboratory, as shown by Fig. 3. Furthermore, these individuals had been subjected to very crowded conditions, initially 3,000 animals in one acclimation crock.

H. azteca and *G. fasciatus* had the highest mortality, and their resistance to lethal temperature declined somewhat during weeks of holding (Fig. 3). In order to reduce heterogeneity from this source, experimental results have not been used if they were based on individuals of either species which had been held in the laboratory for more than a month. It is believed that any changes associated with mortality during acclimation had only a minor effect on resistance-times reported in this work.

DURING TESTS

Another phase of the intolerance of these crustaceans to conditions in the laboratory was relatively short survival-times in some control experiments. Times ranged from about 4 weeks down to 2 or 3 days, depending on species. The possibility of toxicity arising from the apparatus was checked by a series of simultaneous experiments at 20° and oxygen saturation, using *G. pseudolimnaeus*. Under the best conditions which could be provided—swimming free in a large glass jar and provided with food and aeration—survival-times were 6 weeks. Under similar good conditions but without food, as was customary in all experiments, animals starved to death in two weeks. Survival-times were further reduced to one week for routine exposure in the oxygen apparatus and in the temperature bath. Evidence suggested the presence of mildly-toxic materials, probably trace amounts of chlorine in the water of the oxygen apparatus, and a direct-acting poison in the temperature bath. The poison may have been a metal from some part of the apparatus, but later tests failed to discover the source.

Whether toxic materials affected resistance to high temperature was tested with comparable lots of 40 *G. fasciatus*, the control group being held within a glass jar in the same lethal temperature bath. Mean temperatures weighted for time were 31.09° in the bath, and 31.08° in the jar, with actual temperatures always within 0.1° of the means. The progress of mortality with time was almost identical in the two groups of animals. LT50's were 1,320 minutes for those in the bath, and 1,520 minutes for those in the jar. The 95% confidence limits were respectively 790 to 2,200 and 950 to 2,430 minutes. The difference between LT50's was of course not significant. It was concluded that any toxicity of the water did not influence resistance to temperature even during this fairly long experiment. No allowance has been made for such influence in the discussion of other results.

SEX AND WEIGHT

The relative resistance of the sexes was not the same for all four crustaceans, and will be described by species in later sections. Tabulation showed no differ-

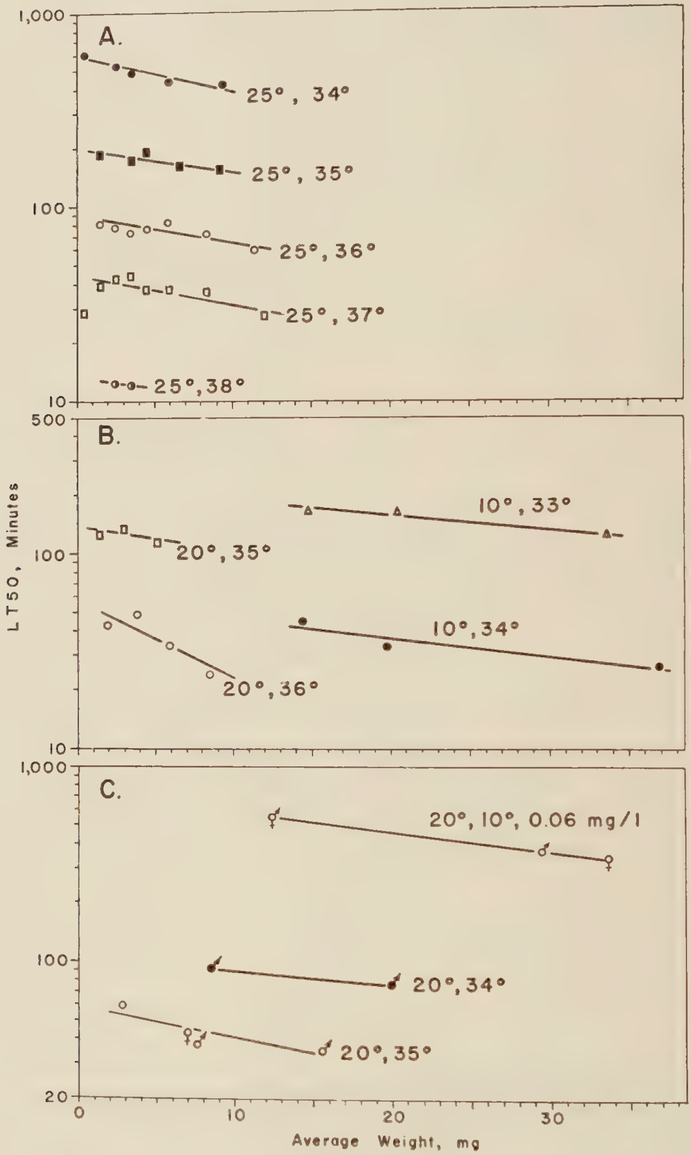

FIG. 2. Effect of weight on resistance-time. **A** and **B** — temperature experiments on *Asellus intermedius*. **C** — temperature and oxygen experiments on *Gammarus fasciatus*. The first number beside each line is the acclimation temperature, and the second is the test temperature. In C, the uppermost line is for an experiment at 0.06 mg/l of dissolved oxygen.

nce in resistance between non-breeding females and those carrying eggs or aving large oostegites. Accordingly results from these categories have been umped.

The effect of weight on resistance is shown in Fig. 2. The general tendency s for the larger animals to have shorter resistance times. In most of the work vhich follows, similar-sized individuals were used within each series of experments.

Not included in Fig. 2 is a comparison of heat-resistance of two sizes of *Iyalella azteca* acclimated at 20° and tested at 35, 36, and 37°. There was no lifference in resistance between small individuals (0.6 to 1.1 mg) and mediumized ones (4 mg). Bovee (1949) concluded that within a similar weight range, arger *H. azteca* were more resistant. However, recalculation of his results to ield LT50's shows no great difference from the present findings.

For other arthropods there have been a variety of conclusions for the effect f size on heat-resistance. Bělehrádek's (1935) list of results obtained by many vorkers shows only that the relation varies with species, stage of life cycle, and riterion of resistance. Spoor (1955) found no difference in temperature resistnce for crayfish between lengths of 17 and 82 mm. However, Kinne (1954) ound that small male *Gammarus duebeni* Lillj. were more resistant than large nales, agreeing with the present findings for *G. fasciatus*. Smaller individuals f two species of mayflies were also more resistant to high temperatures (Whitney, 939).

ATE OF GAIN OF HEAT-RESISTANCE

Animals were brought into the laboratory and kept for a few days at a emperature close to that of their habitat at the time of collecting. Resistanceime was established for a suitable lethal temperature, and comparison with esults presented later showed that each species was acclimated to the initial emperature. Then acclimation temperature was raised quickly and kept at he higher level. Subsequent changes in resistance were followed over a period f days, and are shown in Fig. 3.

One minor irregularity was a decrease in resistance of *G. fasciatus* on the ifth day of the initial holding period. Malfunction of apparatus reduced the emperature in the acclimation bath to 12° for an unknown length of time between he third and fourth days. After correcting the temperature, testing on the ifth day yielded a very heterogeneous response which had the effect of decreasing T50's somewhat. This difficulty would not seem to have a great effect on the eneral conclusions.

A. intermedius raised its acclimation from 20 to 30° in 3 days, an apparent ate of 4° per day. *H. azteca* changed its heat-resistance in 2 days, a rise of 3° er day in acclimation between 14 and 20°. Male *G. fasciatus* raised their cclimation 5° in one day while females took twice as long, giving a rate of 2.5° er day from 15 to 20°.

Among other crustaceans, Spoor (1955) found that increase in heat-resistance f a crayfish was much faster—one day or less when environmental temperature vas raised from 4 to 24°. However acclimation to the lower temperature was

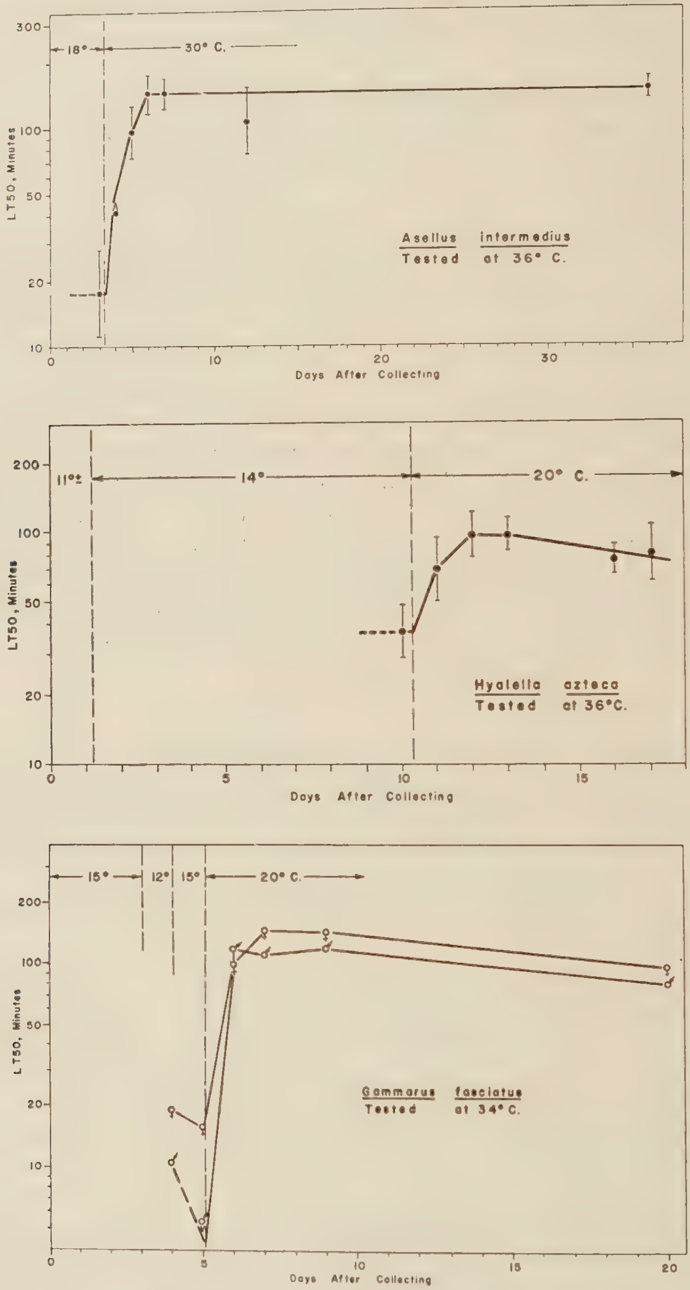

FIG. 3. Increased heat-resistance when acclimation temperature was raised in three species of crustaceans. Tests for successive days were carried out on samples of animals drawn from a group. The history of acclimation temperatures is indicated at the top of each panel.

ot complete. By contrast the American lobster requires at least 24 days to cclimate from 14.5 to 23° (McLeese, 1956). Dickie (1958) determined that he giant scallop raises its acclimation by about 1.7° per day. Many fish raise heir heat-resistance in about one day when the temperatures involved are above 0° (Brett, 1956).

No precise experiments were carried out to show the rate of downward cclimation. However, results described in the next section indicate that *A. ntermedius* lowered its acclimation by at least 1 or 2° per day.

Decrease in resistance during holding was mentioned in a previous section. Resistance of *A. intermedius* did not change during 30 days of holding at 30°, s shown in Fig. 3. It is believed that the straight line drawn through LT50's or days 6, 7, and 36 represents the true situation. This line passes inside the vide 95% confidence limits of the test on the twelfth day, which showed a hetero-eneous response. The other two species lost heat-resistance during holding n the laboratory. For *G. fasciatus*, differences in LT50's for the seventh and wentieth days are close to significance at the 5% level. Differences are not tatistically significant for *H. azteca*, but the trend seems real for both species.

SEASON OF COLLECTING

There are many reports of seasonal changes in lethal levels or physiological ates in aquatic poikilotherms (Fry, 1958; Bullock, 1955). Usually these can e explained by acclimation to seasonal temperature changes, but sometimes hey persist despite laboratory acclimation to a constant temperature. Greater eat-resistance in summer than in winter, independent of acclimation, has been ound in *Planaria* (Schlieper and Bläsing, 1953), an annelid (Kirkberger, 1953), ainbow trout (Keiz, 1953) and goldfish (Hoar, 1955).

In the present study, a set of experiments was carried out to determine vhether laboratory acclimation "erased" all seasonal changes in resistance. Groups of *A. intermedius* were collected in different seasons of 1956, acclinated at 10°, and tested at a series of lethal temperatures. Collections were made n mid-June when water temperatures were 20–25°, in late September at a temperature of 10°, and in December when water temperature was between 0 and °. Time for downward acclimation in the laboratory was only 6 to 8 days for he June animals, and was 26–38 days for the other groups.

Results of these tests are given in Fig. 4. The effect of weight on resistance s shown in two cases for June animals. When this effect is considered, results ndicate that laboratory acclimation eliminated seasonal variation in resistance. The June and December collections provide the best comparison, since weights vere similar, and the difference in habitat temperatures had been extreme. The une animals are slightly more resistant for 3 out of 5 test temperatures, but one of the paired LT50's are significantly different at the 5% level. It was oncluded that temperature resistance of *A. intermedius* was not greatly affected, f at all, by innate seasonal variation, and the possibility of such effects elsewhere n the work has been ignored.

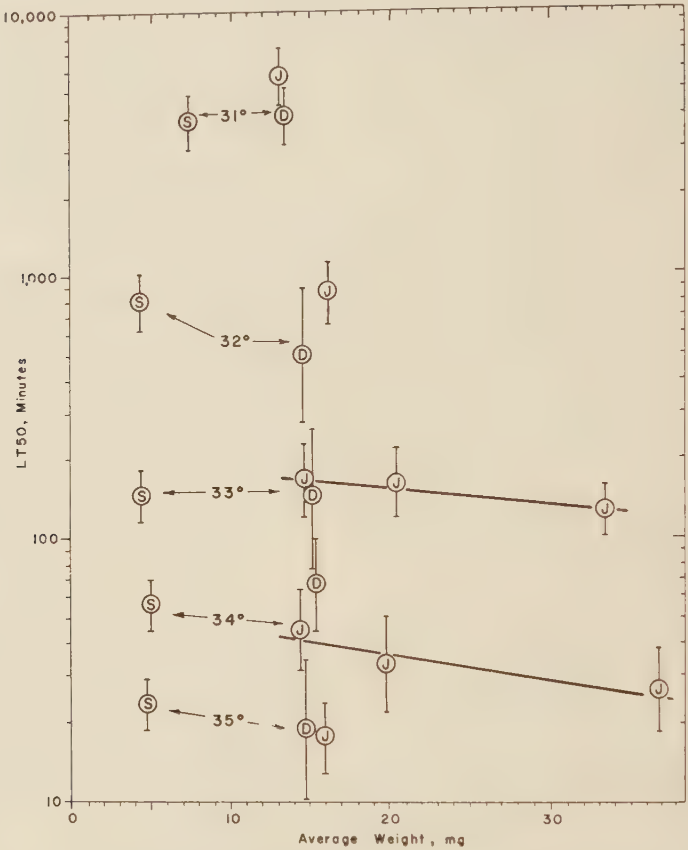

FIG. 4. Lack of seasonal effect on temperature resistance of *Asellus intermedius*. Times to 50% mortality are represented by the initial letters of the months of collecting, June, September, and December. All were acclimated at 10° in the laboratory. Test temperatures are indicated in the body of the graph.

These experiments also indicate that *A. intermedius* lowers its acclimation temperature quickly. The individuals collected in June changed their acclimation from 20 or 25 to 10° in no more than 6 to 8 days. This suggests downward acclimation at a rate of at least 1 to 2.5° per day.

LETHAL HIGH TEMPERATURE

ASELLUS INTERMEDIUS

The heat-resistance of *A. intermedius* was determined for four acclimation temperatures and is given in Fig. 5. Lines were fitted by eye to the points for each acclimation temperature. Separate analyses for males and females showed no difference in resistance, so the data have been united. A rise of 10° in acclimation temperature increased resistance-times by an average of five times, or from

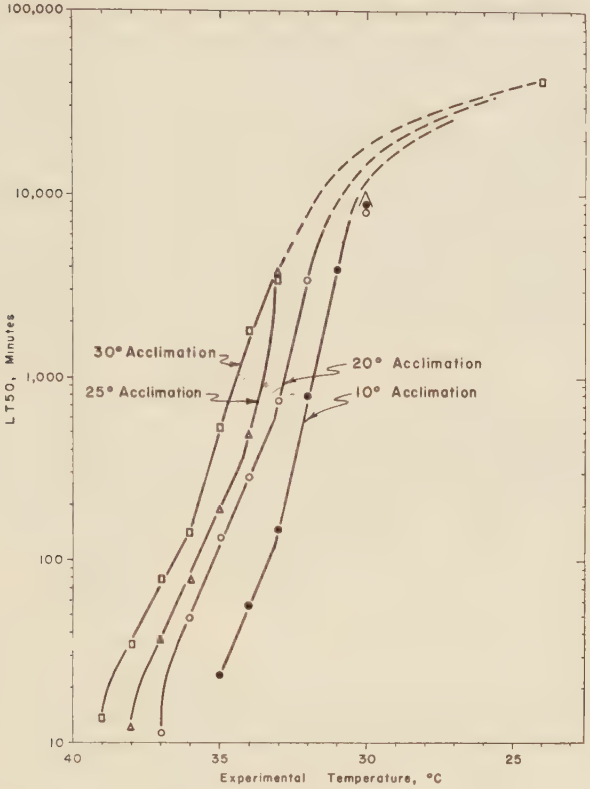

FIG. 5. Times to 50% mortality at high temperatures for *Asellus intermedius*. The arrow placed above the points at 30° experimental temperature indicates that 50% mortality did not occur in one week (10,080 minutes). Based on groups of animals with average weights from 2.6 to 12.1 mg, but mostly close to 5 mg.

nother point of view, raised the lethal temperature by about 1° for equal resist-nce-times. Upward acclimation during a lethal test seems to have occurred or animals acclimated at 25° and tested at 33°. A gain of 5° in acclimation luring the test seems reasonable, since *A. intermedius* can acclimate upwards t 4° per day, and 90% of the individuals in this test were alive at the end of one lay's exposure.

The lowest temperature shown to be lethal was 31° for acclimation at 10°. Vork with fish has usually shown a distinct *upper incipient lethal temperature* for ach acclimation temperature. This can be defined as the temperature below vhich 50% of the organisms live for an indefinite time (Fry, 1947, 1957). In the resent work, survival-times in control experiments, even the four weeks for *A. ntermedius*, were not sufficiently long to estimate incipient lethal temperatures vith accuracy. There have been similar cases in work with fish. Gibson 1954) found no incipient lethal temperature for guppies although some LT50's were 3 weeks. Brett (1952) carried on experiments with chum salmon for more than the usual 10,000 minutes, and found regular mortality at 21°. He credited this to intolerance of fresh water and estimated the incipient lethal temperature as 21.8°. A similar short survival of some controls was found for bluegills (Hart, 1952). Survival for some arbitrary period of time such as 48 hours may be used to approximate the incipient lethal level (McLeese, 1956; Dickie, 1958).

HYALELLA AZTECA

Lethal temperature experiments were conducted on groups of *H. azteca* acclimated at 10 and 20°. There were differences in resistance between males and females, and LT50's are reported separately where possible. The data give no indication of incipient lethal temperatures (Fig. 6).

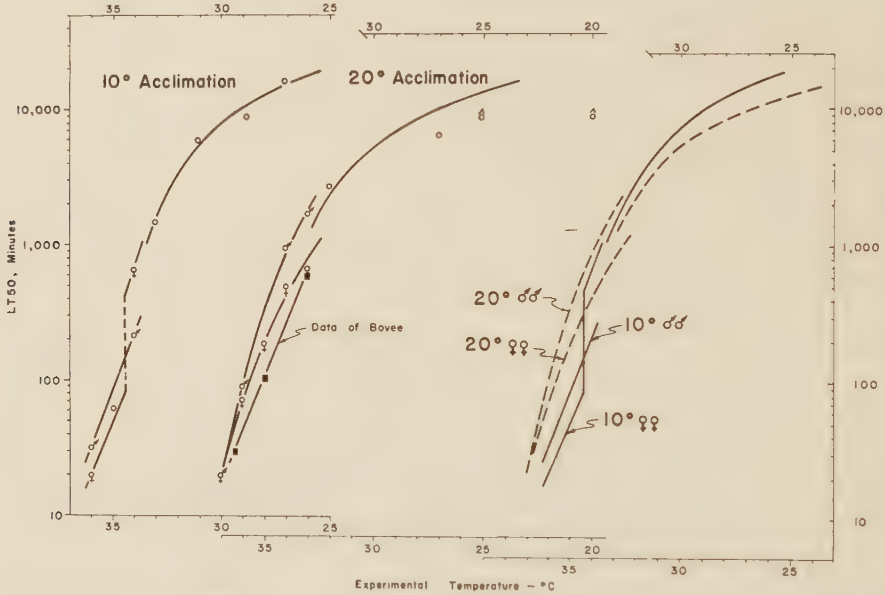

FIG. 6. Times to 50% mortality at high temperatures for *Hyalella azteca*, based on animals with average weights from 3.0 to 4.9 mg. Also shown are approximate LT50's from the data of Bovee (1949) for *H. azteca* of about the same acclimation and weight. The curves are combined in the third panel, with labels to indicate acclimation temperature and sex.

Females acclimated to 10° and tested at 34° gave a "split probit" type of response. Mortality proceeded to about 25% in the first two hours of exposure, then practically ceased for 5 hours, and reached 100% during the last 2 hours. Such results have been obtained by others working with fish (Brett, 1952; Gibson, 1954). It is generally supposed that there are two mechanisms of death, both caused by high temperature in this case. This split probit response is indicated in Fig. 6 by a vertical dashed line. The effect is to make females of 10° acclimation more resistant than males to 34°, although they are less resistant to 36°. For acclimation at 20°, males were consistently more resistant than females.

Split probits were found at 34° for both sexes, but did not greatly influence the overall pattern.

Included in Fig. 6 for comparison are approximate LT50's calculated from the data of Bovee (1949). His animals were acclimated to about 20 or 22°. The two sets of results are close but not identical. This comparison indicates that holding in the laboratory did not have a deleterious effect on heat-resistance. Bovee's *Hyalella* were presumably in normal health since he obtained them daily from a lake, but they show slightly less resistance. Bovee did not recognize any significant differences in resistance between the sexes. Neither was there a statistically significant difference between pairs of LT50's for males and females in the present investigation, but the differences are consistent and seem to be real.

Combining results for the two acclimations shows that acclimation does not have much effect on resistance to temperatures of 33° or less. As an added peculiarity, females acclimated to 10° are more resistant to 34° than those acclimated to 20°. This may be the true situation, but individuals were variable in their response to the two mechanisms of death at 34°. Chance may have played a large part in estimating the LT50 at this temperature.

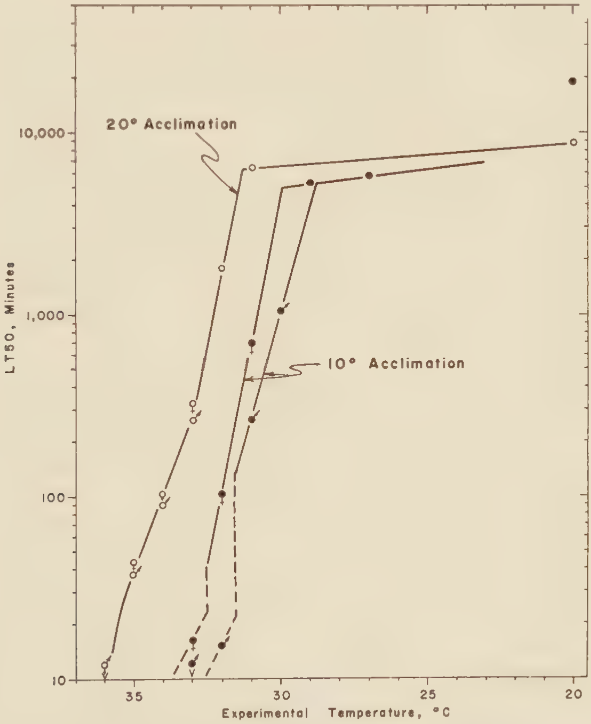

FIG. 7. Times to 50% mortality of *Gammarus fasciatus* at high temperatures. Resistance of the sexes is shown separately where this could be done. Other points are for a mixture of males and females. Based on groups of animals with mean weights from 7 to 15 mg.

GAMMARUS FASCIATUS

Temperature resistance was established for *G. fasciatus* acclimated to 10 and 20°, and results are given in Fig. 7. Irregular results were obtained for 10° acclimation and 32° testing because of split probit responses. Less than 50% of the females died from the faster mechanism of death, but more than 50% of the males, giving a great difference in LT50's although the general reaction was similar. Females are more resistant than males in all cases where there is a comparison, but the difference is small for 20° acclimation. Kinne (1954) found that male *Gammarus duebeni* seemed to be more resistant than females, just the opposite situation.

A rise of 10° in acclimation caused a large increase in resistance-times, generally between 10 and 30 times. Survival of controls was only 1 to 2 weeks causing sharp breaks in the lines relating temperature to resistance-time. These breaks at about 4 days indicate that there was little interaction between direct lethal effects of temperature and mortality due to holding conditions.

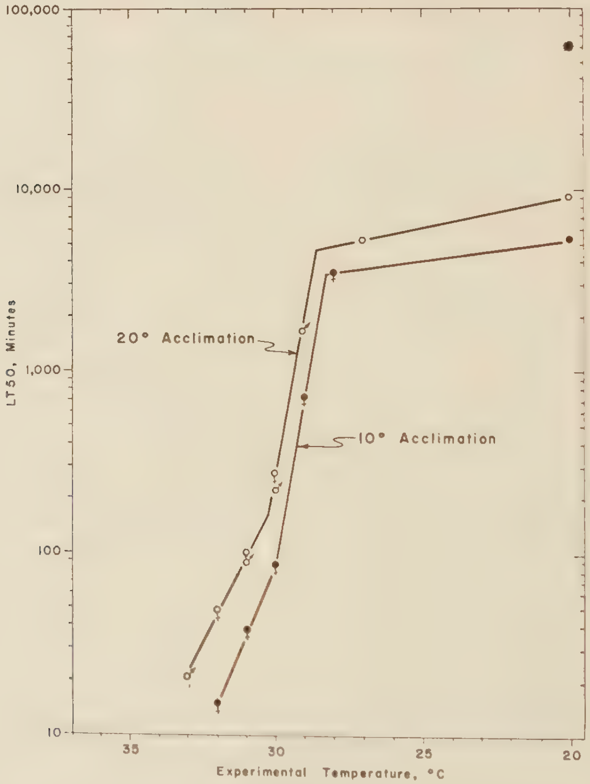

FIG. 8. Times to 50% mortality of *Gammarus pseudolimnaeus* at high temperatures. The asterisk at 20° represents a control experiment under very favourable holding conditions, and is discussed in the text.

AMMARUS PSEUDOLIMNAEUS

The general pattern of temperature resistance of *G. pseudolimnaeus*, shown n Fig. 8, is similar to that of *G. fasciatus*, although temperatures are 2 or 3° ower. The relation of lethal temperature to time was apparently interrupted t about 4,000 minutes by mortality from other laboratory conditions. Survivalime was about 6 weeks in a control experiment under very good holding conditions. This experiment was discussed earlier, and had the animals swimming ree in a large glass jar and provided with food. It is possible that incipient ethal temperatures could have been determined by carrying out all tests this vay.

For many experimental temperatures a satisfactory estimate of the LT50 ould be made for only one sex, since there were few individuals of the other sex. n the two cases where there is a comparison, females seem to be slightly more esistant as was the case with *G. fasciatus*.

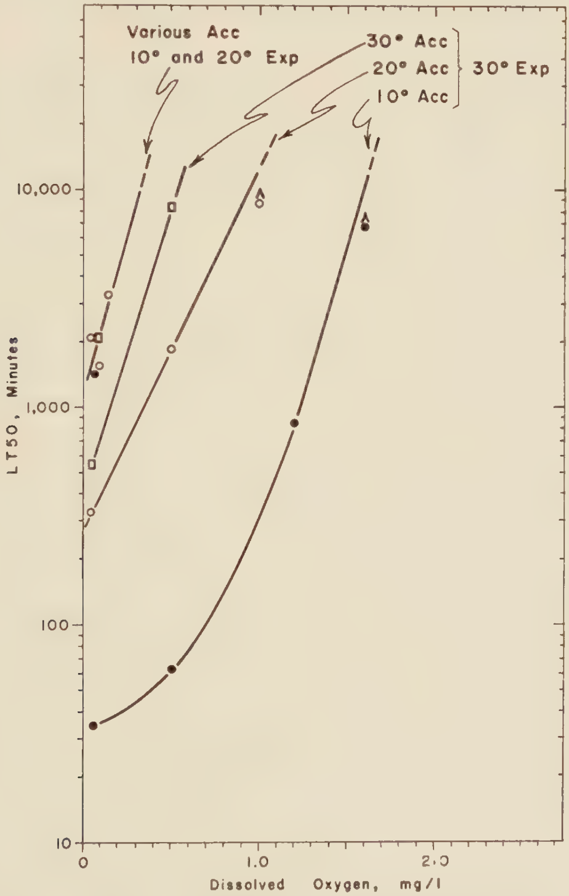

FIG. 9. Times to 50% mortality of *Asellus intermedius* exposed to reduced levels of dissolved oxygen. In the body of the graph, "Acc" means acclimation temperature, and "Exp" signifies experimental temperature.

A rise of 10° in acclimation increased resistance-times by an average of only three times. The effect of acclimation was probably even less than this, since large animals of 37–50 mg average weight were used for 10° acclimation, while more usual weights averaging 12–23 mg were used for 20° acclimation. Smaller animals for 10° acclimation probably would have been more resistant, bringing results even closer to those for 20° acclimation.

LETHAL LOW OXYGEN

ASELLUS INTERMEDIUS

For this species, experiments with low oxygen were carried out at nine temperature combinations, obtained by using 10, 20, and 30° both for acclimation and tests. However, for tests at 10 and 20°, resistance to low oxygen was so great that no influence of temperature could be detected. A single line has been drawn through the points representing these experiments in Fig. 9. At these two experimental temperatures, all groups of animals survived 0.5 mg/l of oxygen for more than a week.

When animals were acclimated and tested at 30°, their resistance was almost as great as that of individuals tested at 10° and 20°. For example, the LT50 for 0.5 mg/l of oxygen was 8,500 minutes, or almost 6 days. As would be expected, testing at 30° after acclimation to lower temperatures decreased resistance to low oxygen. However, even for acclimation at 10° and testing at 30°, the most severe combination of temperatures used, *A. intermedius* survived for about one week in 1.6 mg/l of dissolved oxygen.

There did not seem to be a significant difference in resistance between males and females. In 6 of the 7 cases where comparisons could be made, resistance was almost identical. The effect of size is not known. Mean weights of the groups of *A. intermedius* used in low oxygen work were from 5 mg to 14 mg.

HYALELLA AZTECA

Groups of *Hyalella* were acclimated to 10 or 20° and exposed to reduced oxygen at temperatures of 10, 20, and 30°. Comparable results for males and females in six experiments showed no trend for either sex to be more resistant. The groups of animals had average weights from 1.5–4.2 mg.

As would be expected, survival at a given level of oxygen was longer for the lower experimental temperatures, as shown in Fig. 10. The effect of acclimation temperature seems to be variable but is not fully documented. On the whole *H. azteca* is quite resistant to reduced oxygen supply. When acclimated to 10°, the levels of oxygen which allowed survival for about a week at test temperatures of 10, 20, and 30° were 0.5, 1.0, and 1.7 mg/l. Even an increase in oxygen to air-saturation did not increase survival-time greatly at 20°.

GAMMARUS FASCIATUS

The same temperature combinations were used as for *Hyalella*. Females were more resistant than males in all nine experiments which had results for both sexes. Some of the differences were small and could not be indicated in Fig. 11.

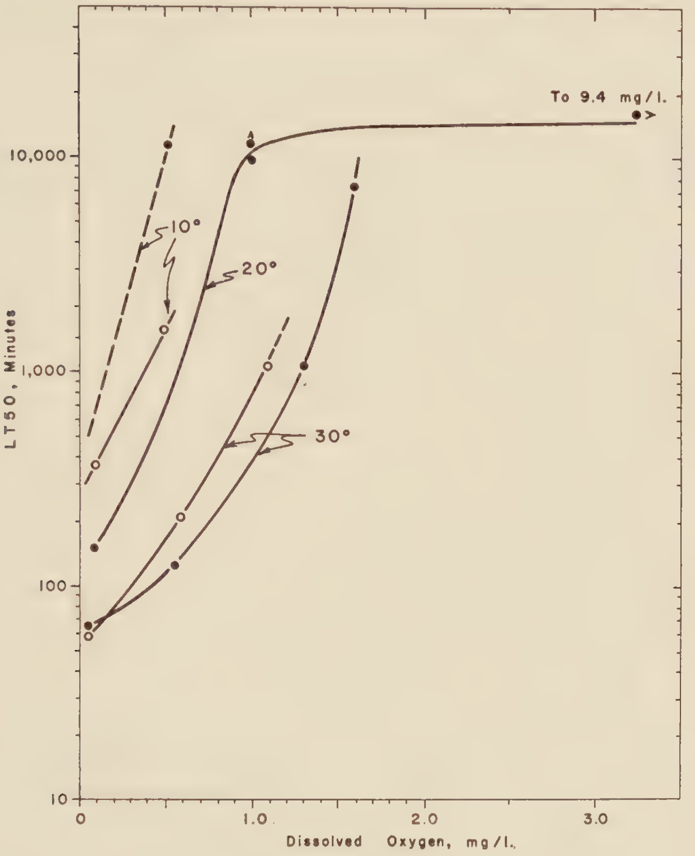

FIG. 10. Times to 50% mortality of *Hyalella azteca* exposed to reduced levels of dissolved oxygen. Experimental temperatures are indicated in the body of the graph. Closed circles represent acclimation at 10°, open circles at 20°.

The pattern of resistance to low oxygen supply is reasonable and regular. A rise of 10° in acclimation temperature increased resistance-times by a factor of only 1.4 or less. As in the two species discussed previously, *G. fasciatus* was able to survive for some time in almost completely deoxygenated water. For example, the LT50 for exposure to 0.06 mg/l of oxygen was 3 hours for acclimation and testing at 20°. Survival in control experiments was only 2 to 3 days, apparently because of toxicity of the experimental water. Variation in this toxicity may account for longer survival in the control experiment at 20° than in the one at 10°.

Because of this short survival, detailed interpretation of these results is not justified, but it seems clear that reduction of oxygen below about 4 mg/l had an effect on resistance-times.

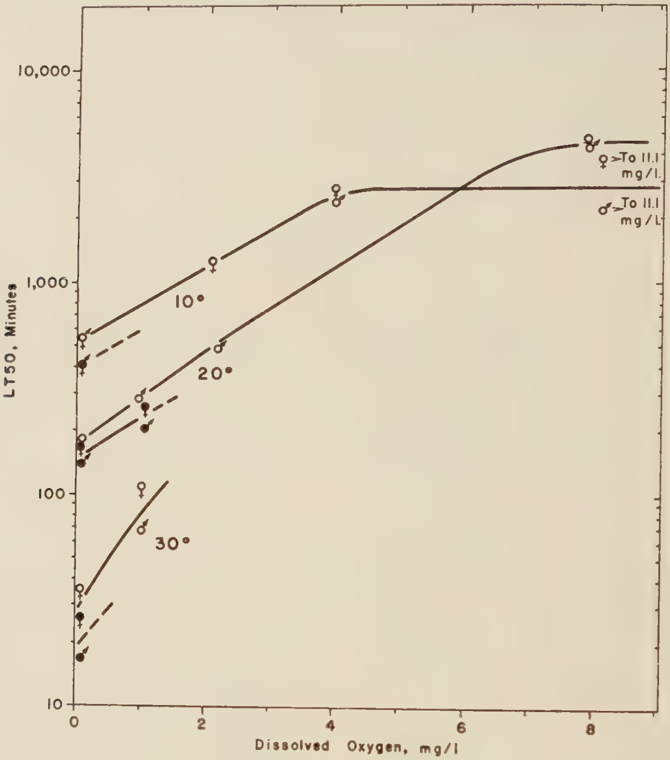

FIG. 11. Times to 50% mortality of *Gammarus fasciatus* exposed to reduced levels of dissolved oxygen. Test temperatures are indicated in the body of the graph. Closed circles are for acclimation at 10°, open circles for acclimation at 20°.

GAMMARUS PSEUDOLIMNAEUS

Temperature conditions were the same as for the other two amphipods. Insufficient numbers of animals were used to compare resistance of males and females. Average weights of the groups of animals were from 9 to 16 mg.

There were some inconsistencies such as crossing of lines drawn to fit results for the two acclimations, and separate panels have been used in Fig. 12 to avoid confusion. For 10° acclimation, LT50's at 4 mg/l of oxygen are the same for two test temperatures. Since such results seem to be in error as a result of heterogeneity in different groups of *G. pseudolimnaeus*, conclusions should not be drawn from minor differences.

Among major differences it is clear that *G. pseudolimnaeus* died more quickly than the other species when exposed to nearly deoxygenated water (0.06–0.09 mg/l). At this low oxygen supply, the LT50 was less than 15 minutes at 30°, was about one hour at 20°, and 2 or 3 hours at 10°. Resistance-times were decreased at oxygen concentrations up to 4 or 5 mg/l, compared with control experiments at near-saturation values for oxygen.

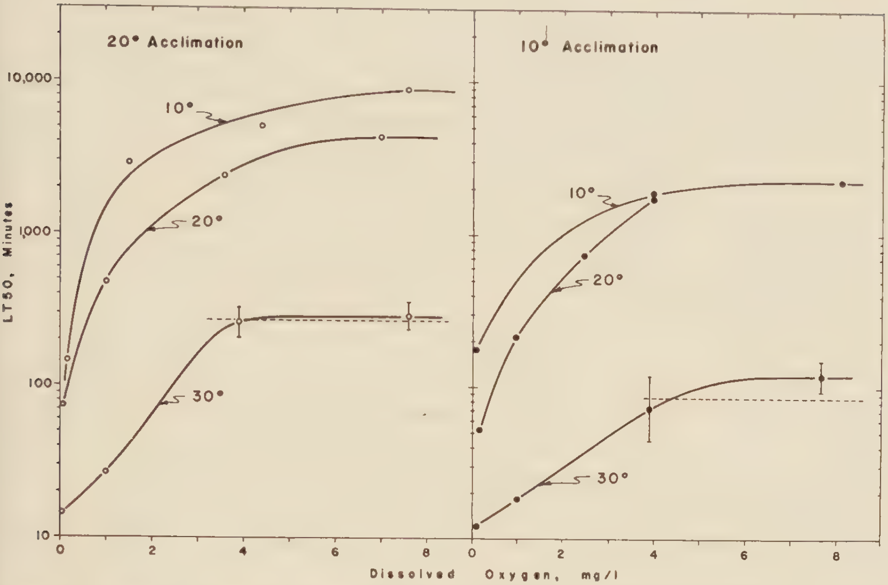

FIG. 12. Times to 50% mortality of *Gammarus pseudolimnaeus* exposed to reduced levels of dissolved oxygen. The lines are labelled with the test temperatures. The horizontal dashed lines show the time for death at 30° as determined in lethal temperature experiments.

Of special interest are the experiments at 30°, a lethal temperature for *G. seudolimnaeus*. Horizontal dashed lines in Fig. 12 indicate LT50's for 30° as etermined in the lethal temperature work. The LT50's for 3.9 and 7.6 mg/l of issolved oxygen are very close to the LT50's for temperature experiments. For 0° acclimation the three resistance-times are almost identical, and for 10° acclimaon, none are significantly different at the 5% probability level. It may be oncluded that heat-resistance of *G. pseudolimnaeus* was not greatly influenced y reduction of the oxygen to 3.9 mg/l, approximately half of the air-saturation alue. McLeese (1956) did not find this for the lobster. He indicates a curilinear merging of lethal effects, with heat-resistance lowered appreciably at 4 g/l of dissolved oxygen.

DISCUSSION AND CONCLUSIONS

As a criterion of resistance which could be applied to all four species, it was ecided to use the "24-hour LC50". This can be defined as the environmental vel of the lethal factor which kills 50% of the individuals in 24 hours. LC50 gnifies "lethal concentration for 50% of individuals". This criterion based n 24 hours does not have the same value as an incipient lethal level, but is useful r comparative purposes.

IGH TEMPERATURE

The 24-hour LC50's for heat-resistance, taken from Fig. 5 to 8, are shown in ig. 13 which is patterned after the thermal tolerance diagrams of Fry (1947).

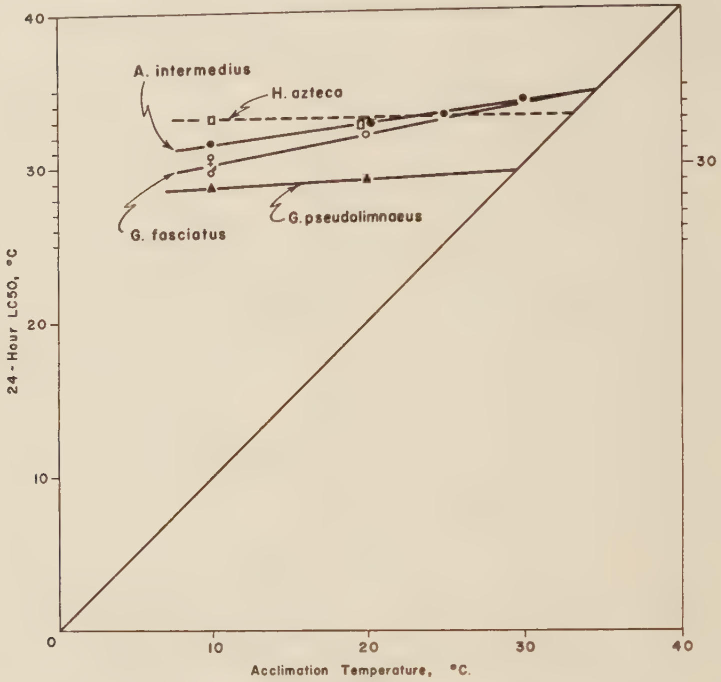

FIG. 13. The relation between acclimation temperature and the high temperature which causes 50% mortality in 24 hours for the four species of freshwater crustaceans. The diagonal line indicates points where experimental temperature equals acclimation temperature.

The line drawn through each set of LC50 values intercepts the diagonal construction line where acclimation and experimental temperatures are equal This is the highest temperature to which the 24-hour LC50 can be raised b acclimation. It is designated hereafter as the "ultimate 24-hour LC50", sinc it is comparable to the "ultimate upper incipient lethal temperature" of Fr (1947).

Acclimation has the greatest effect in *G. fasciatus* and *A. intermedius*. Fo a rise of 10° in acclimation temperature, 24-hour LC50's increased by 1.9 and 1.3° respectively. The increase for *G. pseudolimnaeus* is only 0.5°.

The 24-hour LC50 for *H. azteca* acclimated at 20° could not be estimate with great accuracy. In Fig. 13 a horizontal line has been drawn through th value for 10° acclimation. If correct, this would signify that acclimation ha no effect on resistance. There is some precedent for such a result since therma tolerance diagrams of fish generally exhibit a plateau near the central construction line. In the guppy, this plateau apparently extends over the whole biokineti range (Gibson, 1954). Relations seem fairly clear for the other species. It i possible that plateaus might occur. If present, the ultimate 24-hour LC50 fo *A. intermedius* and *G. pseudolimnaeus* would not be reduced more than 0.5°, bu a reduction of 2.5° could occur for *G. fasciatus.*

Ultimate 24-hour LC50 values read from Fig. 13 are 34.6° for both *A. inter-edius* and *G. fasciatus.* For *H. azteca* the value is apparently about 33.2°, nd for *G. pseudolimnaeus* it is lower, at 29.6°. The ultimate 48-hour LC50 alues have been estimated by the same procedures, and are not much lower. or the species in the same order, they are 33.6, 33.0, 32, and 29.3°.

The relative rank of the species according to their resistance agrees in eneral with expectations from their ecology. *A. intermedius*, *H. azteca*, and *. fasciatus* have all been found in water which becomes warm in summer, whereas *. pseudolimnaeus* is typical of cool waters. However the differences are not as eat as might be expected, the ultimate 24-hour LC50 of *G. pseudolimnaeus* eing only 5° lower than that of the most resistant species.

To show whether temperature resistance is important in determining the pe of habitat which these species can utilize, absolute values for summer mperatures in fresh water are needed. Ellis (1937) summarized 4,500 summer ream temperatures representing most parts of the United States and southern anada. Mountainous headwaters were excluded. In view of high summer air mperatures, it is surprising that 95% of the water temperatures were below 5°. Unpublished observations made by the author on a small river in southern ntario also indicate that water temperatures are lower than might be expected. his river was shallow, slow, and mostly unshaded, but the maximum tempera-ure attained during the summer was 29.2°. The daily maxima for July and ugust averaged only 25.4°, and average temperature for any day was usually ° less than the maximum.

Ultimate 24-hour LC50's of three of the species used in this study were 33° more, much higher than stream temperatures mentioned above. For these ustaceans, there is a considerable "safety margin" for direct lethal effects of mperature. The fourth species, *G. pseudolimnaeus*, had an ultimate 24-hour C50 of 29.6° and would apparently survive temperatures in most rivers and reams of North America. Yet this species seems to be restricted to cool waters ich as the stream where it was collected, which had maximum summer tem-eratures of about 18°. Although the 24-hour LC50 is lower than those of arm-water species, it is not truly indicative of the levels of temperature in the abitat. A conclusion drawn for certain fishes by Brett (1956) seems to apply) *G. pseudolimnaeus* very well: "Some other property or attribute of the organ-m, roughly reflected by the upper lethal temperature, must be operating as ie restricting factor in distribution". Such an attribute might concern favour-ble or optimum temperatures for various life functions. An example has been rovided by McLeese and Wilder (1958) who measured activity of the lobster. n a considerable part of the zone where temperature was non-lethal, continued xistence of the lobster was not possible because of complete inactivity.

Figure 14 compares 24-hour LC50 values for a number of aquatic poikilotherms. alues for the lobster and the two fishes are interpolated from published graphs. esults for *A. intermedius* and *G. pseudolimnaeus* are the extremes from the resent investigation, but lie in a fairly central position. The crayfish *Orconectes isticus* has a resistance about 2° higher than *A. intermedius* while the resistance

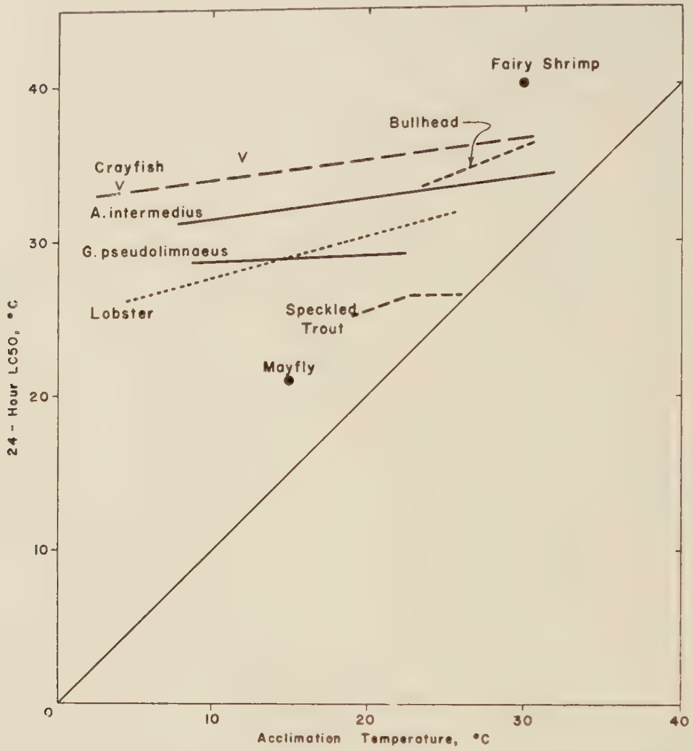

FIG. 14. Comparison of the temperatures resisted for 24 hours by different aquatic poikilotherms. Lines for *Asellus intermedius* and *Gammarus pseudolimnaeus* taken from Fig. 13. The other organisms, and sources of data from which the lines were constructed, are given below.

Fairy shrimp	*Streptocephalus seali* Ryder	Moore, 1955
Crayfish	*Orconectes rusticus* (Girard)	Spoor, 1955
Bullhead	*Ameiurus nebulosus* (LeSueur)	Hart, 1952
Lobster	*Homarus americanus* Milne-Edwards	McLeese, 1956
Speckled trout	*Salvelinus fontinalis* (Mitchill)	Fry *et al.*, 1946
Mayfly	*Baetis rhodani* Pictet	Whitney, 1939

of the lobster is similar to that of *G. pseudolimnaeus.* Acclimation has more effect in the lobster. Among fish which have been tested, the bullhead is one of the most tolerant of high temperatures, while the speckled trout is one of the least tolerant. The extreme values found in the literature were for a southern fairy shrimp and a mayfly characteristic of running waters. The acclimation temperatures represented for these last two are probably accurate to within 5°.

LOW OXYGEN

The 24-hour LC50's for low oxygen are shown in Fig. 15. There are separate curves for each acclimation temperature of each species. A lower position in the graph indicates greater resistance.

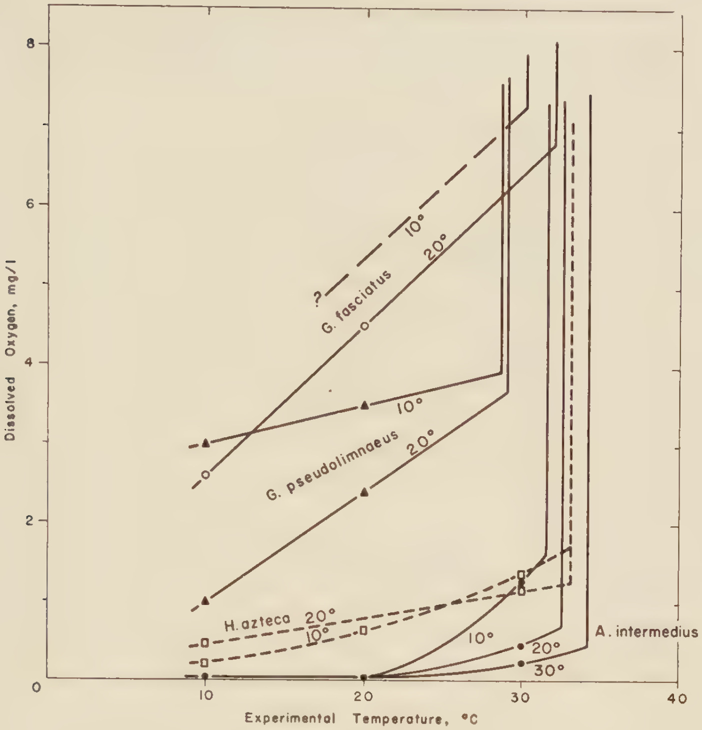

Fig. 15. The relation between temperature and the level of dissolved oxygen which causes 50% mortality in 24 hours for four species of crustaceans. The relation is terminated on the right by heat-death. Acclimation temperatures are indicated in the body of the graph.

The general order of resistance for the species is clear. Comparison seems st at 20° for both acclimation and testing. For this temperature, the 24-hour C50 was 0.03 mg/l of dissolved oxygen for *A. intermedius*, 0.7 mg/l for *H. teca*, 2.2 mg/l for *G. pseudolimnaeus*, and 4.3 mg/l for *G. fasciatus*.

The extreme resistance of *Asellus intermedius* agrees with expectations from ological information. Several members of the genus are notable for occurring polluted and deoxygenated waters. Specifically, field observations (Sprague, 54) showed that *A. intermedius* survived 9 hours of exposure to oxygen levels tween 0.6 and 1 mg/l with temperatures averaging 20°. The present work ows that *A. intermedius* can resist even lower levels of oxygen for 24 hours.

Field observations (Gaufin, 1958; Sprague, 1954) show that *H. azteca* somenes lives in waters having almost this degree of oxygen deficiency. The ecies was present but rare in the location described above for *A. intermedius*. ne prevailing levels of 0.6 to 1 mg/l of dissolved oxygen for 9 hours come very ose to the 24-hour LC50 of *H. azteca*, which is 0.7 mg/l. It seems likely that e rarity of *H. azteca* at this particular location was related to direct lethal fects of low oxygen. This seems especially probable since *H. azteca* was common at a downstream location with slightly higher concentrations of dissolved oxygen. Sampling indicated that oxygen was typically reduced to 1.0 mg/l for about three hours before dawn, which is somewhat less severe than the 24-hour LC50 for *Hyalella*.

No ecological information is available for oxygen relations of *Gammarus pseudolimnaeus*.

The LC50 values for *G. fasciatus* appear high. The lobster, for comparison, would not seem to need great resistance to low dissolved oxygen, yet survives for 48 hours in 1.1 mg/l of oxygen (McLeese, 1956). However, the LC50 for *G. fasciatus* does agree with ecological information as far as could be ascertained. There is a comparative lack of records for the occurrence of *G. fasciatus* in deoxygenated water, even though this is a common species. The most severe case discovered in the literature which may apply to *G. fasciatus* is that of Gaufin (1958), who found *Gammarus* sp. living where the minimum level of oxygen was 40% of saturation. The 24-hour LC50 of 4.5 mg/l is a little less than 50% of the saturation value at 20°.

Thus it is seen that *A. intermedius*, *H. azteca*, and perhaps *G. fasciatus*, may live in habitats where dissolved oxygen comes close to lethal levels. Therefore direct lethal effects of low oxygen seem to be important in determining which waters are suitable for these species.

As a final note, it must be added that although lethal oxygen relations seem to be of direct importance, this does not imply that mere survival levels make for a suitable habitat. Much of the time it would be necessary to have higher oxygen content to allow the animal to cope with other stresses in the environment.

SUMMARY

1. The crustaceans used were the isopod *Asellus intermedius* Forbes, and the amphipods *Hyalella azteca* (Saussure), *Gammarus fasciatus* Say, and *Gammarus pseudolimnaeus* Bousfield.
2. Acclimation temperatures used before testing were 10° and 20° for all species, plus 30° for *A. intermedius*.
3. Resistance to high temperature decreased with size in *A. intermedius* and *G. fasciatus*, over a weight-range of 1-35 mg. Small and medium-sized *H. azteca* were about equal in resistance.
4. Female *Gammarus* were generally more resistant than males to high temperature and low oxygen. Resistance of the sexes was equal in *A. intermedius*, while differences were evident in *H. azteca*, but variable.
5. The three species tested could raise their acclimation temperature by 2.5 to 5° per day, judging by heat-resistance at acclimations of 14° and higher.
6. Seasonal variation in heat-resistance was not apparent after *A. intermedius* had been acclimated in the laboratory.

There was considerable mortality during holding in the laboratory, and survival-times in some control experiments were short. Neither of these difficulties seriously affected the resistance which is reported.

A rise in acclimation from 10° to 20° increased the temperature resisted for 24 hours by 1.9° in *G. fasciatus*, 1.3° in *A. intermedius*, 0.5° in *G. pseudolimnaeus*, and apparently not at all in *H. azteca*.

Estimates of the highest 24-hour lethal temperatures which could be obtained by raising acclimation were 34.6° for *A. intermedius* and *G. fasciatus*, 33.2° for *H. azteca*, and 29.6° for *G. pseudolimnaeus*.

Differences in heat resistance between species are not as great as might be expected from their habitats. Temperature-resistance seems greater than necessary for survival in nature, especially for *G. pseudolimnaeus*, which is a cool-water species.

Concentrations of oxygen causing 50% mortality in 24 hours were 0.03 mg/l for *A. intermedius*, 0.7 mg/l for *H. azteca*, 2.2 mg/l for *G. pseudolimnaeus*, and 4.3 mg/l for *G. fasciatus*. These oxygen values were for acclimation and testing at 20°, and changed for other combinations of temperatures.

Resistance to low oxygen fits field observations fairly closely, and explains presence or absence of these species in polluted waters.

ACKNOWLEDGMENTS

I would like to thank Dr F. P. Ide of the University of Toronto for guidance all phases of this study. Facilities for graduate study were provided by J. Dymond, Professor Emeritus, and Dr K. C. Fisher, Chairman of the Depart-nt of Zoology. The work was made possible by research grants to Dr Ide m the Ontario Research Foundation, and scholarships from the National search Council.

Helpful suggestions from Drs F. E. J. Fry and L. Butler of the University Toronto are greatly appreciated. I would also like to acknowledge stimulus d help given by fellow-scientists of the Fisheries Research Board of Canada St. Andrews. Dr E. L. Bousfield, of the National Museum of Canada, kindly ntified the amphipods used in this study, and Dr J. G. Mackin, of Texas ricultural and Mechanical Research Foundation, identified the isopod.

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The Biology and Taxonomy of the Burbot, *Lota lota*, in Heming Lake, Manitoba[1]

By G. H. Lawler

Fisheries Research Board of Canada
Biological Station, London, Ont.

ABSTRACT

Vital statistics on the burbot, *Lota lota*, of Heming Lake, Manitoba were collected over a period of several years. Age, weight and length data are presented. The maximum age of fish in the sample was 8 years. The largest fish (for which no age was determined) was 33 inches long and weighed 11 pounds. The growth of Heming Lake burbot appears slower than in Lakes Erie and Simcoe. The main types of food found in 1,441 burbot stomachs, in order of highest incidence, were yellow perch, ninespine sticklebacks and crayfish. Winter food was almost exclusively ninespine sticklebacks. The average number of eggs per female was approximately ½ million. Spawning probably occurred in early March.

The morphometry of the burbot of Heming Lake was described on a sample of over 100 fish. The inadequacy of most of the published data made comparisons with other populations almost impossible. It was concluded that, until statistically significant samples are obtained over the burbot's range, there is insufficient evidence for recognizing subspecific differences and that all should be referred to as *Lota lota* (Linnaeus).

INTRODUCTION

For several years the Fisheries Research Board of Canada carried out an intensive fishing program at Heming Lake in northern Manitoba (Lat. 55°N, Long. 101°W), Canada. In the early years of the fishery the burbot, *Lota lota*, was only taken occasionally, but with increased fishing effort in later years there was an appreciable increase in the number of burbot in the catch. As a routine part of the study, data on length, weight, sex, age and food were collected and the results are reported herein. Although similar data have been previously published on the burbot in North America, none were from an area so far north.

The genus *Lota* is circumpolar in its distribution. Those from eastern Siberia and Alaska have been described as *Lota lota leptura* by Hubbs and Schultz (1941). The remainder of the range in Europe and Asia is inhabited by the subspecies *Lota lota lota*, and in Canada and the northern United States by *Lota lota lacustris*, formerly *Lota lota maculosa* (see Speirs, 1952). Lindsey (1956) did not believe that there was sufficient evidence for recognizing subspecific differences between Alaskan and either European or eastern American forms and stated, "Without further data on what is evidently a complex situation, all should be referred to as *Lota lota* (Linnaeus)."

It is believed that the subsequent description of the Heming Lake burbot population and comparisons of the taxonomic characters with previously published descriptions will assist in better understanding the taxonomic status of the burbot.

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[1] Received for publication September 18, 1962.

J. Fish. Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

METHODS OF CAPTURE

Most fish were captured with linen, cotton and, since 1950, nylon gill nets ranging in mesh size from 1 inch (2.54 cm) to 5½ inches (14 cm) stretched measure. In the early years of the study, hoop nets of 2½-inch (6.35 cm) mesh, stretched measure, were fished daily in several of the creeks of the lake. Occasionally shallow regions were poisoned with 5% emulsifiable rotenone and samples of burbot too small to be caught by the other gears were obtained. Burbot were rarely taken in shore seines.

AGE AND GROWTH

The age and growth study is based on the examination of 547 specimens collected in 1958 and 1960. The total length was measured from the tip of the snout to the farthest tip of the caudal fin. All measurements were of fresh specimens. Otoliths were either stored in 50% glycerin or left in the dry state in storage envelopes. Many of the stored otoliths were too opaque to transmit light for age determinations, but after heat treating (Lawler and McRae, 1961) the annual rings were quite evident.

Ages were assigned according to methods used by Martin (1941). The fish in the samples ranged in age from one to eight years and were from 5.8–20 inches (14.6–50.8 cm) in length. The age composition of the catch in the two years is shown in Table I. Although young-of-the-year fish were taken in each of several years by poisoning, no otoliths were aged for inclusion here. These younger fish in mid-summer averaged 3 inches (7.6 cm) in length.

Seventy-three percent of the sample is represented by 3- and 4-year-old fish. The 2- and 5-year-old fish together constituted 17% of the catch. It is noted that there are some differences in the age composition between the years 1958 and 1960. In 1958 the 4- and 5-year-old fish were dominant in the catch, while in 1960 the 3- and 4-year-old fish were present in largest numbers with the 3-year-old fish most abundant. This difference can be partly explained by changes in fishing effort. To reduce the pike, *Esox lucius*, population in the lake, the fishing effort was intensified annually, beginning about 1955, with the result that the average size of all species decreased. As the average size of fish

TABLE I. Age composition (percent) of the burbot catch in Heming Lake in the years 1958 and 1960 (actual numbers in parentheses).

Year of capture	Age (in completed years)								Total
	I	II	III	IV	V	VI	VII	VIII	
1958	14.7 (20)	16.9 (23)	15.4 (21)	30.8 (42)	22.0 (30)	. . .	. . .	. . .	136
1960	. . .	4.1 (17)	64.2 (264)	17.5 (72)	5.3 (22)	4.4 (18)	4.4 (18)	0.24 (1)	411
Both years combined	3.6 (20)	7.3 (40)	52.1 (285)	20.8 (114)	9.5 (52)	3.3 (18)	3.3 (18)	0.18 (1)	548

ecreased, the mesh size of the nets used for catching the fish was decreased and he total yardage of nets in the lake was increased. Thus with intensive fishing ore young fish appeared in the catch. The same explanation is offered for the creased numbers of older fish in the catch in 1960. As the amount of fishing as increased, the larger fish became more vulnerable to capture. The reason hat 1-year-old fish appear in the catch in 1958 and not in 1960 is the result of hore poisoning in the former year and no poisoning in 1960. The 1-year-old sh were not large enough to be caught in the nets then in use.

The maximum age in the current sample was 8 years. It would be expected hat this is not the maximum age that could be reached in Heming Lake, as the verage size in the present study is considerably smaller than it was before the ntensive fishing began. Unfortunately, there are no ages available for the fish

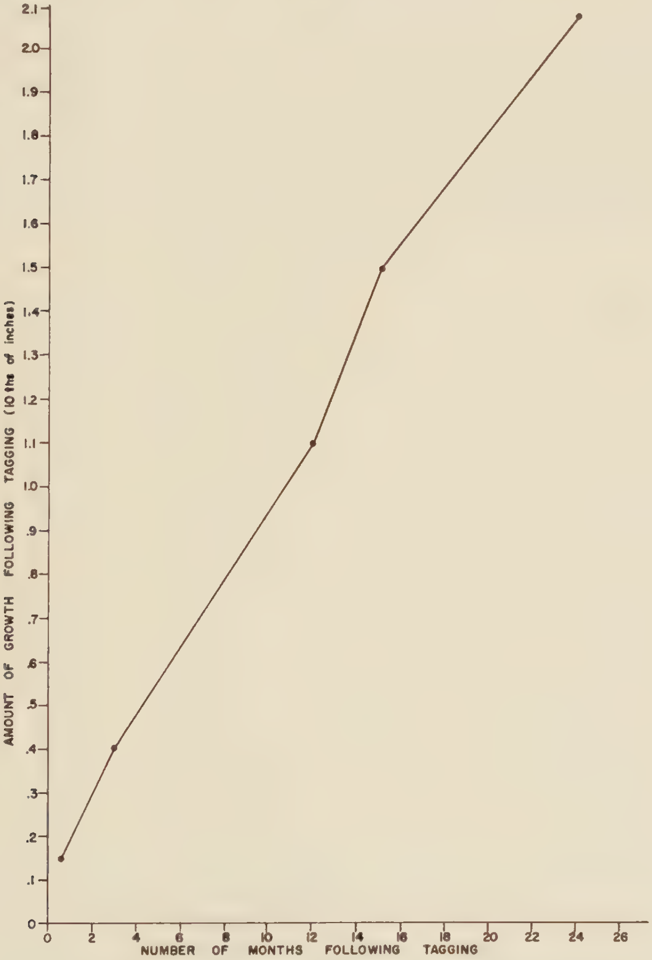


FIG. 1. Growth of Heming Lake burbot as shown by the increase in length between time of tagging and subsequent recapture.

caught earlier. For example, in 1947 a female burbot weighing 11 lb (4.9 kg) and measuring 33 inches (83.8 cm) was caught; in the same year several burbot $3\frac{1}{2}$–$5\frac{1}{2}$ lb (1.6–2.4 kg) were taken. McCrimmon (1956) stated that the largest burbot taken from Lake Simcoe was 33 inches (83.8 cm) long, weighed $9\frac{1}{2}$ lb (4.3 kg) and was 13 years old. These larger burbot from Heming Lake were possibly older than 8 years of age.

The average length in inches (1 inch = 2.54 centimeters) at various ages follow: 1 year (5.8); 2 years (9.7); 3 years (11.0); 4 years (12.7); 5 years (14.4); 6 years (15.7); 7 years (16.9); 8 years (18.3).

From these averages it is calculated that the average growth increment, excluding the growth in the very early years, is approximately 1.4 inches (3.6 cm) per year. This figure agrees well with growth data obtained from tagged and recaptured fish. The amount of growth accrued between time of tagging and time of recapture is illustrated in Fig. 1. It is seen that the burbot grow in length approximately $\frac{1}{10}$ of an inch (0.25 cm) per month, or at an average rate of 1.3 inches (3.3 cm) per year. Fish that had been tagged showed growth increments of $\frac{4}{10}$ inch (1.0 cm), $1\frac{1}{10}$ inches (2.8 cm), and $2\frac{1}{10}$ inches (5.3 cm) respectively, 3, 12 and 24 months later. As the annual growth increment as determined from the age analysis agrees so closely with the actual growth as indicated by the tag and recapture data, it should be possible to assign ages with

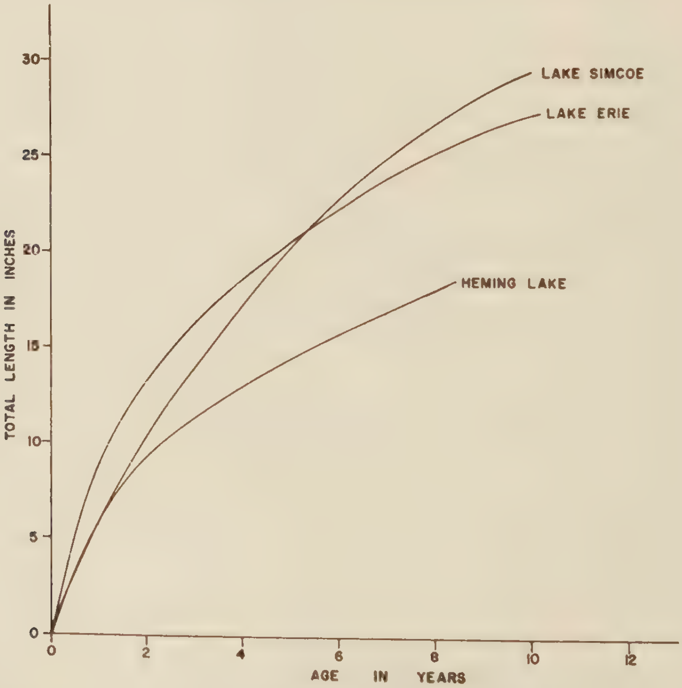


FIG. 2. Growth curves of the burbot in Lakes Erie, Simcoe and Heming. Data for Lake Erie extracted from Clemens (1951) and for Lake Simcoe from McCrimmon (1956).

ertain limitations to fish for which age material is missing. For example, the 3-inch (83.8-cm) burbot mentioned previously is possibly at least 18 years of ge.

The growth of Heming Lake burbot is somewhat slower than in Lake Erie nd Lake Simcoe, as shown by the comparison of lengths at various ages in ig. 2.

The relationship between length and weight, based on a sample of over 100 sh of both sexes, is shown in Fig. 3. The length-weight relationship can be xpressed by the equation:

$$\log W = -2.52 + 3.164 \log L$$

here W equals weight in ounces (1 oz = 28.35 g) and L equals total length in ches.

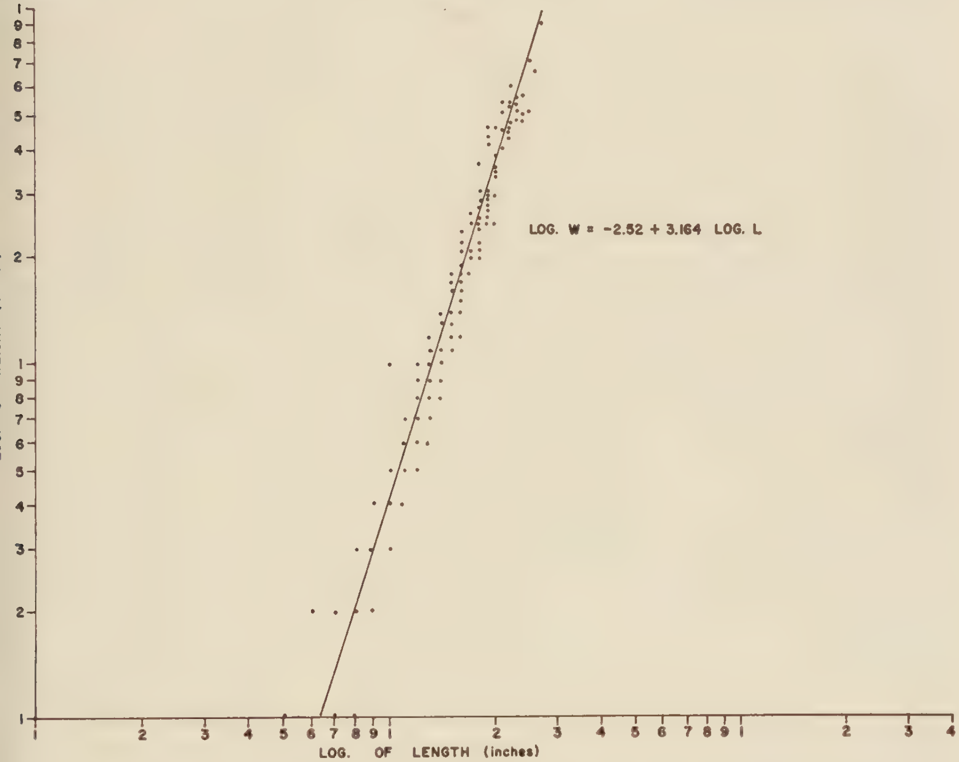


FIG. 3. Length–weight relationship of Heming Lake burbot.

FOOD

Between the years 1952 and 1960 a total of 1,441 stomachs were examined o determine the types of food consumed by burbot. Of these 969, or 67.2%, ontained food. With the exception of a few fish captured in the winter of 953–54, most of the data shown in Table II were recorded from fish caught etween May and October and will be considered as representing the summer eeding habits of burbot. For a general description of the food types eaten by

TABLE II. Number and percentage of 1,441 burbot stomachs containing various food items; data from Heming Lake from 1952 to 1954 and 1957 to 1960 (percentage shown in parentheses).

Item	1952	1953	1954	1957	1958	1959	1960	Combined
Total number stomachs:	14	31	20	129	258	596	393	1,441
Empty stomachs:	. . .	. . .	1 (5)	25 (19)	89 (34)	182 (30)	175 (44)	472 (33)
No. of stomachs with food:	14 (100)	31 (100)	19 (95)	104 (81)	169 (65)	414 (69)	218 (55)	969 (67)
Fish								
Perca flavescens	. . .	3 (10)	3 (16)	59 (57)	9 (5)	116 (28)	54 (25)	244 (25)
Percopsis omiscomaycus	13 (93)	20 (64)	10 (53)	12 (11)	22 (13)	26 (6)	20 (9)	123 (13)
Pungitius pungitius	2 (14)	15 (48)	6 (31)	15 (14)	40 (24)	98 (24)	29 (13)	205 (21)
Catostomus commersoni	1 (7)	4 (13)	6 (31)	3 (3)	5 (3)	2 (0)	3 (1)	24 (2)
Cottus cognatus	. . .	. . .	. . .	. . .	. . .	3 (1)	2 (1)	5 (1)
Notropis hudsonius	. . .	1 (3)	. . .	. . .	3 (2)	3 (1)	2 (1)	9 (1)
Esox lucius	. . .	. . .	1 (5)	. . .	3 (2)	1 (0)	. . .	5 (1)
Etheostoma nigrum	. . .	. . .	. . .	3 (3)	. . .	3 (1)	. . .	6 (1)
Unidentified fish	1 (7)	1 (3)	3 (16)	10 (10)	38 (22)	174 (42)	84 (38)	311 (32)
Invertebrates								
Hexagenia sp.	1 (7)	. . .	. . .	15 (14)	13 (8)	46 (11)	5 (2)	80 (8)
Cambarus sp.	5 (36)	8 (26)	1 (5)	13 (12)	34 (20)	55 (13)	33 (15)	149 (15)
Odonata	. . .	. . .	. . .	5 (5)	2 (1)	5 (1)	3 (1)	15 (2)
Hirudinea	. . .	. . .	. . .	. . .	2 (1)	2 (0)	2 (1)	6 (1)
Unidentified insects	. . .	3 (10)	. . .	1 (1)	10 (6)	. . .	2 (1)	16 (2)
Misc. (including fish eggs, vegetable matter, debris)	. . .	. . .	. . .	1 (1)	4 (2)	10 (2)	5 (2)	20 (2)

ırbot, the combined data shown in the last column will be used. Yellow perch, *erca flavescens*, were identified in 25% of the stomachs with food. No explana- on is offered for the decrease in the amount of perch consumed in 1958, as there d not appear to be any shortage of perch or perch fry in the total catch of fish r that year. The ninespine stickleback, *Pungitius pungitius*, was found in)% of the stomachs with food. The only other fish which contributed signifi- ıntly was the troutperch, *Percopsis omiscomaycus*, which occurred in 9% of the omachs. The remaining 5 species of fish occurred rarely in the diet. A high ercentage of the fish eaten by the burbot had to be classified as fish remains, food digestion had proceeded too far for positive identification. These fish ere mainly fry and were most likely perch. Of the invertebrate organisms, ie crayfish (*Cambarus* sp.) was found in 15% of the stomachs, and thus ranked gh among the individual items which occurred most frequently in the food of ie burbot. Mayfly (*Hexagenia*) larvae occurred in 9% of the stomachs. The maining invertebrates and the miscellaneous matter which included fish eggs, getable matter and debris did not occur frequently enough to be considered ıportant food items.

Although there are not much data on the winter feeding habits of the burbot, iere are enough to indicate that some seasonal differences exist. Examination the 1953–54 data showed that during the summer months the burbot ate ainly troutperch, crayfish, sucker (*Catostomus commersoni*) and sticklebacks, that order. In the fall, perch and sticklebacks were the dominant food types, ıt in winter the diet was found to be exclusively ninespine sticklebacks. The gh incidence of sticklebacks possibly resulted from a greater availability rather ıan a seasonal preference, as the ninespine stickleback is a northern cold water sh and is probably more active at lower water temperatures than other species ith a more southerly distribution.

The relation of food type to size or age of the burbot is concerned only with sh older than yearlings, as no smaller fish were examined. Among the youngest sh examined, 2 years old and up to 9 inches (22.8 cm) in length, fish of other ecies and crayfish were the dominant items. The older fish from 3 to 7 years age ate mostly fish and crayfish. Aquatic insects were observed occasionally fish up to 4 years of age and a length of 15 inches (38.1 cm), but were not found larger or older fish.

It is unfortunate that volumetric analyses were not made, as the qualitative ıta do not give any indication of the amount of food consumed. The burbot a voracious eater, as shown by the great numbers of fish appearing in individual omachs. It was not unusual to find 80 or 100 troutperch or ninespine stickle- ıck or as many as 14 crayfish in one stomach.

It is interesting to note that of the 15 species of fish present in Heming Lake, e burbot showed evidence of having eaten only 8 species. Of these, the perch, outperch and ninespine stickleback were by far the most common. The cker, which became very abundant in the period 1957–60, occurred in very w numbers in the stomachs. The absence of suckers, Catostomidae, in the et of burbot was noted in the results of Clemens (1951b) and Van Oosten and

Deason (1938). It would appear that the sucker is not a preferred food type. Pike which were at peak abundance during this period were rarely found in the stomachs. One explanation for the apparent scarcity of pike in the burbot diet is based on differences in behaviour. The pike does not usually travel in groups and tends to hold one position unless attacked or frightened by something in its territory—at this time it will dart either to or away from the object. The burbot, on the other hand, swims with a reptilian movement and is more likely to prey on fish which tend to swarm and are active swimmers, such as young perch or coregonines. The logical conclusions to be drawn from these data are that in Heming Lake the burbot appears to prefer some types of fish to others regardless of abundance, shows a preference for crayfish among the invertebrates and is mainly a fish eater during the winter months, feeding exclusively on stickleback.

SPAWNING, SEX RATIO AND FECUNDITY

During part of the winter 1953–54, burbot gonads were examined to determine the time of spawning in Heming Lake. In late November and December the burbot were most plentiful in the deeper waters of the lake and were caught in bottom-set nets. No fishing was carried out in January. In February the fish appeared to be moving to shallower water and were taken in large numbers inshore. By February 15 milt could be forced from the male burbot, but pressure on the ovaries would not cause the release of eggs. One week later the same condition was observed. By February 28 the milt appeared to be running relatively freely; however, the eggs were still not running freely from the females. The water temperature at this time ranged from 32.5°F (0.3°C) at the surface, just below the ice, to 39°F (3.9°C) at the bottom. Winter fishing operations were concluded in the first few days of March, so it can only be speculated on the evidence available that, as the males were ripe, the females would soon follow suit and spawning probably occurred in early March. No spawning was observed nor were any spawning areas located.

When burbot were next examined in early May, all mature males and females showed the spent condition.

McCrimmon (1959) reported that the burbot in Lake Simcoe spawn in late January and early February, while Clemens (1951a) states that the spawning season in Lake Erie occurs in the last week of March and the first week in April. Robins and Deubler (1955), citing several references to the spawning time of burbot throughout its range, list spawning times from November to May.

The sex ratio of 811 burbot for the years 1958, 1959 and 1960 was 1.6 females: 1 male. For individual years the ratios were as follows:

1958 — 2.7 females: 1 male
1959 — 0.8 female: 1 male
1960 — 1.8 females: 1 male

No explanation can be offered for the low number of females in the catch in 1959. With the exception of 1959, females appeared more abundant than males.

It is interesting to contrast the above sex ratios with those obtained just ior to spawning. The following data have been grouped in 5-day intervals to ovide adequate samples for comparison:

Feb. 10–14	1 female: 1 male
15–19	4 females: 6 males
20–24	2 females: 3 males
25–29	4 females: 7 males
Mar. 1–5	4 females: 6 males
Average ratio:	0.6 female: 1 male

In the first five days of spring fishing (May 19–23, 1954), the burbot had ompleted spawning and the sex ratio at that time was 4 females: 1 male. Thus ore males were noted around spawning time than the average sex ratio would dicate. Both sexes were equally vulnerable to the fishing gear and as the nets ere not being consciously fished on or near burbot spawning grounds, one planation that can be offered for the change to a predominance of males in id-winter is that they become more active near spawning time and thus are ore likely to be caught in fixed fishing gear.

Ovaries were collected from 12 burbot during February and March, 1954, st before the time of spawning. The ovaries were wrapped in cheesecloth d preserved in 10% formalin. To count the eggs the ovaries were removed om the formalin and the excess fluid was absorbed on blotting paper. Ex-ssive ovarian membrane, blood vessels, etc., were removed with forceps. The aries were placed on a balance and the weight (A) was recorded in grams. he ovaries were then broken up and the weight (B) of a sample of the eggs presentative of several regions of the ovaries was obtained. The number of gs in the sample (C) was counted and from the equation $\frac{B}{A} = \frac{C}{X}$, X, the total umber of eggs per female was computed. The egg diameter was obtained by acing 10 randomly selected eggs on a millimetric rule and calculating the erage of the readings to the nearest ½ millimeter. These data are shown in able III.

The number of eggs per female ranged from 74,800 to 1,362,000 and averaged most ½ million eggs per individual for the sample. The number of eggs appears oportional to the size of the fish. The egg numbers at the various lengths pear somewhat greater than the number given by Bjorn (1940) for Wyoming rbot.

Based on only three observations, the average diameter of the eggs of the rbot was 0.5 mm.

COLOURATION AND HABITAT

The back and sides of the adult burbot are olivaceous to dark brown in lour. This colour is overlain with distinct web-like, vermiculate markings d spots of darker brown or black. The belly is creamish. There is considerable riation in the colour within the same body of water, which may reflect the

TABLE III. Size of fish, egg diameter and number of eggs for 12 Heming Lake burbot examined during February and March 1954.

Total length	Weight	Average diameter	Number of eggs
inches	*ounces*		
11.5	7	...	109,338
12.5	10	...	149,338
13.0	8	...	176,939
16.0	20	...	74,810
16.0	34	...	278,733
17.5	24	...	538,599
18.0	26	0.5	223,868
18.0	38	...	684,036
19.3	40	0.5	671,231
19.5	42	...	578,203
23.5	62	0.6	530,441
25.3	98	...	1,362,077
Av.: 17.5	34	0.5	448,134

effect of the particular area or habitat in which it has been resident. The very young and juvenile burbot is purplish-black in colour, with a whitish colouring on the underside. The mottled effect, so apparent on the back and sides of the adult, is not evident.

In the early spring the larger burbot were plentiful in hoop nets set in creek mouths and in shore-set gill nets. During the warm summer months the larger burbot is found usually in the deepest parts of the lake and only occasionally is it taken in nets in the shallower water. Large burbot sometimes occur inshore in late fall when the water temperature has declined, but are usually found in the deeper water. Young-of-the-year and yearlings, however, are frequently found along rocky shores during shore poisoning operations. The burbot were often difficult to find following poisoning, as they attempted to burrow between rocks and into cavities along the bank.

PEDUNCLE RATIO

In separating *L. l. leptura*, *L. l. lota* and *L. l. lacustris*, Hubbs and Schultz (1941) used a ratio, the distance from notch at end of dorsal fin to the end of the vertebral column divided by the distance between the notches at the ends of the dorsal and anal fins. They distinguished *L. l. leptura* from *L. l. lota* and *L. l. lacustris* on the basis of a marked difference in the shape of the caudal peduncle. The isocercal caudal region of *L. l. leptura* has a long, narrow, acute posterior end and this is not so marked in the other two forms.

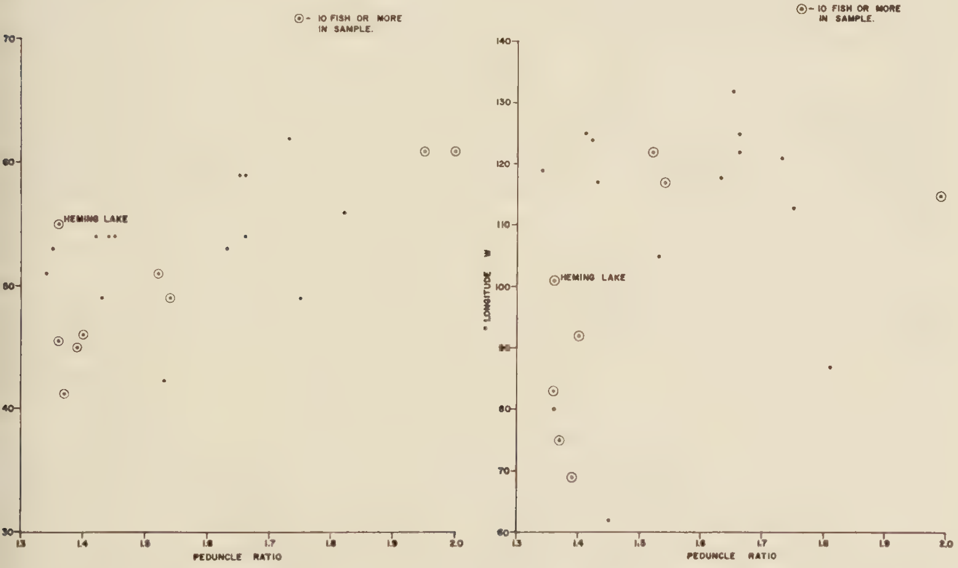
The peduncle ratios obtained for Heming Lake burbot are given in Table IV. The mean peduncle ratio for this population was 1.36 and the range was from 1.0 to 1.7. One fish had a peduncle ratio of 2.1, but was excluded from the analysis as the vertebrae and hypural complex appeared atypical in this specimen.

ABLE IV. Ratio of peduncle length to peduncle height in Heming Lake burbot. (Size range of burbot 170–529 mm standard length.)

	Peduncle ratio								No. of specimens	Mean
	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7		
requency	1	3	18	43	36	25	7	3	136	1.36

Vhen these data are compared with similar data based on adequate samples eported by Lindsey (1956), the peduncle ratio for the Heming Lake population grees favorably with the ratios obtained on populations from eastern and north-entral North America and Europe. The average peduncle ratio is lower than n the Great Slave Lake and Alaskan populations, but there is a considerable mount of overlap.

Lindsey (1956) believed that the peduncle ratio tends within North America o increase towards the north and towards the west, and points out that latiudinal and longitudinal trends are difficult to separate. When the Heming ake data and the data from Lindsey (1956) were plotted against longitude and atitude (Fig. 4), a different interpretation is possible. It is seen that the peduncle atio remains about the same (1.3–1.4), with increasing longitudes up to approxinately 120°W. At 120°W longitude there are still some populations with low audal peduncle ratios, but at this juncture the range in average caudal peduncle atios becomes much wider and the average is generally higher. It almost ppears as though there are two lines coverging at this point.



IG. 4. Relationship between caudal peduncle ratio and degrees latitute north and degrees longitude west for several burbot populations.

When this ratio is plotted against latitude, a definite relationship is not established. There is a weak trend to higher peduncle ratio with increasing latitude, but the points are widely scattered. The Heming Lake population (55°N latitude) which has a low average ratio, is only separated from the populations having the highest ratios by approximately 7° latitude. As the populations found 10° latitude south of Heming Lake had ratios of 1.3:1.4, it would have been expected that the Heming Lake population would have had an average of approximately 1.6. Perhaps this indicates a distinct or different post-glacial source of repopulation for burbot in the Hudson Bay drainage, or merely emphasizes the fact that the sample sizes in most instances are too small to take into account the variability of this diagnostic character over the range of the fish's distribution.

PECTORAL LENGTH

The length of the pectoral fin has been used as one of the taxonomic characters for separating the forms of *Lota*. The length of the pectoral fin of 136 Heming Lake burbot ranged from 21–68 mm, with a mean length of 38.2 mm. The length of the fin is proportional to the size of the fish, and the relationship between standard length of fish and length of pectoral fin can be expressed by the following equation: $\text{Log } Y = 1.025 \text{ Log } L - 0.922$. As the ratio used by Hubbs and Schultz (1941) was not obtained for the Heming Lake fish, only average pectoral lengths were used for comparison with other populations.

Hubbs and Schultz (1941) stated that, "On the average both American forms have shorter pectoral fins than the typical European species". When average pectoral lengths of Heming Lake burbot at various sizes were compared with the published data of Hubbs and Schultz (1941), it was not apparent that the European form possessed longer pectoral fins. The tip of the pectoral fin, however, did fall decidedly short of the level of the origin of the dorsal fin and this was one of the characters used to separate the European form from the North American form. Population differences based on this character may not be of great significance, as the difference depends as much on the position of the first dorsal as it does on the length of the pectoral fin. Fish of the same size from different populations could have pectoral fins of the same size, but if the first dorsal was located more anterior in one than in the other, they could not be distinguished by the length of the pectoral fin. The Heming Lake burbot, particularly in the smaller size range, did appear to have longer pectoral fins than the burbot from the Great Lakes St. Lawrence River region. The measurements could not be fairly compared with the data on *L. l. leptura*, because of the paucity of specimens.

MERISTIC CHARACTERS

VERTEBRAL COUNTS AND VERTEBRAL ABNORMALITIES

Vertebral counts were made on 137 burbot, but 15 were excluded because of abnormalities. The vertebral counts are shown in Table V.

A sample of these vertebrae was checked by Dr W. B. Scott, Royal Ontario Museum of Zoology, Toronto. His counts agreed favorably with those made by the writer.

ABLE V. Frequency of vertebrae in 122 burbot from Heming Lake, Manitoba. (Standard length of fish 170–529 mm.)

	Number of vertebrae											No. of specimens	Mean
	53	54	55	56	57	58	59	60	61	62	63		
equency	1	...	...	2	2	10	21	36	26	16	2	122	59.9

It is difficult to make comparisons with other populations due to lack of ublished data. Hubbs and Schultz (1941) indicate that *L. l. lota* and *L. l. aculosa* = *L. l. lacustris* have approximately the same number of vertebrae, ut that *L. l. leptura* has on the average more vertebrae. The average vertebral umber for the Heming Lake population agrees more closely with *L. l. lota* than either *L. l. lacustris* or *L. l. leptura*.

Vertebral abnormalities in wild populations of several species of fish have een described by Scott (1951), McHugh and Barraclough (1951), Lawler (1961) nd others. Abnormalities in wild populations appear to vary from 4% to 10 11% and involve simple fusion of two centra to highly complex masses of five entra or more. In the present study, 10.9% of the 137 specimens used for ertebral counts had abnormalities which ranged from 1 to 3 or more fused ertebrae.

IN RAYS

Fin ray counts were made for 100 first dorsal, second dorsal, anal and pelvic ns, and 97 pectoral fins of burbot (Table VI). To avoid any ambiguity in umeration, the fins were clipped near the base and the clipped ends of the rays ere readily visible.

There are very few data for comparing pectoral and pelvic fin ray numbers different burbot populations.

A comparison of the ranges and means of dorsal and anal rays (Fig. 5) for everal populations from both North America and Europe shows differences, but e small number of counts for most populations prevents drawing taxonomic onclusions.

RANCHIOSTEGAL RAYS

Branchiostegal rays were counted on the left side of the isthmus of 100 fish. here was little variation among the fish. The range was from 6 to 8, with a ean of 7.2.

ILL RAKERS

Gill rakers were counted on 136 specimens. The range was from 7 to 11, ith a mean of 8.8. These data are presented in Table VII for comparison with ll raker counts of burbot from the Susquehanna River system (data from obins and Deubler, 1955).

No significant difference is evident between these widely separated populaons.

TABLE VI. Fin ray counts of *Lota* from Heming Lake, Manitoba. (Standard length range 170–569 mm.)

	Number of Rays																					No. of specimens	Mean
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22					
Dorsal I	...	...	...	3	1	7	13	30	23	16	4	3	...	...	...	...	...	...				100	12.4
Pelvic	1	28	70	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...				100	6.7
Pectoral	...	...	...	...	...	...	...	...	...	...	...	...	8	22	35	27	5	...				97	19.8
	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78		
Dorsal II	...	...	1	...	...	...	1	2	1	4	4	9	8	17	17	9	9	8	6	2	2	100	71.6
Anal	1	2	2	2	3	4	8	15	7	11	14	10	10	3	5	2	...	...	1	...	...	100	66.8

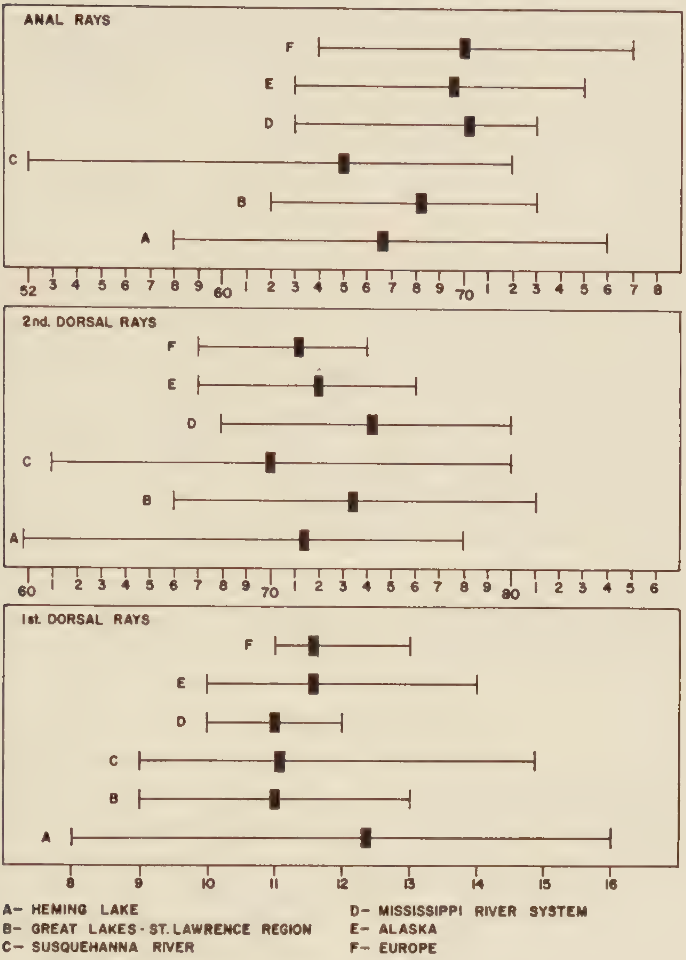


FIG. 5. Comparison of range in anal and dorsal ray counts for several burbot populations. (Mean count shown by heavy bar.)

YLORIC CAECA

Pyloric caeca were counted on 101 specimens in the size range 170–569 mm· he caecal counts ranged from 37 to 96, with a mean of 55. There was only eak association between size of fish and number of caeca. The range in number f caeca for most size groups was extremely wide. For 32 specimens of the usquehanna River system, Robins and Deubler (1955) reported a mean count f 33.3 pyloric caeca, with a range of 20–54. The only other comparison is with ie data of Bean (1884), who listed pyloric caeca counts ranging from 36 to 188, ith the highest counts from specimens from the Yukon River.

TABLE VII. Gill raker counts of burbot from Heming Lake, Manitoba, and from the Susquehanna River system, New York State.

	Number of gill rakers					No. of specimens	Mean
	7	8	9	10	11		
Heming Lake	1	44	71	12	8	136	8.8
Susquehanna River system	2	8	11	4	...	25	8.7

OTHER BIOMETRIC DATA

Interorbital distance, eye diameter, length of maxillary and length of barbel were measured for over 100 specimens. When the data for each were arranged in size groups, it was obvious that measurement of each character was related directly to the length of the fish. In order to demonstrate the relationship and to obtain a regression line to describe the relationship, the measurements of body parts and lengths of fish were plotted on double logarithmic paper and the best straight line was drawn through the points (data on file at Biological Station, London, Ont.). The following equations were derived:

Barbel length × standard length	$\log Y = 1.582 \log L - 0.2755$
Eye diameter × standard length	$\log Y = 0.852 \log L - 1.198$
Interorbital distance × standard length	$\log Y = 1.306 \log L - 2.137$
Maxillary length × standard length	$\log Y = 1.257 \log L - 1.697$

DISCUSSION

It is obvious from the preceding description of the Heming Lake burbot population that adequate samples from other geographic areas are necessary to understand the distribution of the species and the possibility of subspecific differentiation. Many of the characters used in systematic studies vary in proportion to the size of the fish. These characters are of little use in distinguishing populations unless the samples include the total size range or unless sampling is restricted to a study of adults. If the caudal peduncle ratio can be considered a valid descriptive character, then there is some evidence that *L. l. leptura* is a distinct subspecies. The factors influencing a change in this character are unknown, but might include size, sexual maturity and environment; thus there is some doubt concerning its suitability as a good taxonomic character. The mean vertebral number in the Heming Lake population was lower than the mean count for *L. l. leptura*, but as there is a general tendency for vertebral numbers to increase with more northerly distribution, differences in this character would not be sufficient to establish a subspecies.

As far as other characters are concerned, it would appear that there are no differences significant enough to separate *L. l. lota* and *L. l. lacustris* with the limited data available. The data collected on the Heming Lake population indicates for some characters a closer association with *L. l. lota* than with *L. l. lacustris*, but in most cases there is considerable overlap. The only evidence for separating *L. l. lota* and *L. l. lacustris* is the apparent greater pectoral length of

l. lota. This difference does not appear to be based on the length of the ectoral fin, but rather on the predorsal distance. Until samples of statistically gnificant size are acquired, extending over the total range of the burbot's stribution, all populations including that of Heming Lake should be referred as *Lota lota* (Linnaeus) as suggested by Lindsey (1956).

ACKNOWLEDGMENTS

The valuable assistance of Mr G. P. McRae in the field, in the compilation the data and in determining the ages of the fish is gratefully acknowledged. Ir R. S. Williams assisted in determining the number of eggs. Messrs C. D. oster and B. E. Meeker assisted in making the taxonomic measurements. Dr . B. Scott reviewed the manuscript and offered valuable criticisms.

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Biological Changes in Herring Stocks Following An Epizootic[1]

By S. N. Tibbo and T. R. Graham[2]

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

Herring landings in the Chaleur Bay area of the Gulf of St. Lawrence declined from 25 million lb (11,340 metric tons) in 1947 to 12 million lb (5443 metric tons) in 1959. The decline is attributed to lower levels of abundance resulting from mortalities caused by a fungus (*Ichthyosporidium hoferi*) disease which reached epidemic proportions during the mid 1950's. Data obtained during the periods 1946–48 and 1960–61 are compared and show mean lengths of herring have remained unchanged, mean ages have decreased, growth rates have increased, fewer year-classes are represented and relative abundance of autumn-hatched fish has increased.

INTRODUCTION

Heavy and widespread mortalities of herring in the Gulf of St. Lawrence were reported by fishermen and by Protection Officers of the Department of Fisheries of Canada in the late spring and early summer of 1954. Herring were behaving abnormally, swimming lethargically near the surface in inshore areas, especially in harbours near wharves and breakwaters. Dead herring were seen floating at the surface and washed up on the beaches throughout most of the inshore areas of the southwestern Gulf from Gaspé to Cape Breton and along the west coast of Newfoundland. Offshore, large quantities of partially decomposed herring were taken on bottom by otter trawlers. Mortalities started about mid-May near the end of the fishery for spring-spawning herring. They reached a peak in June, continued at about the same level throughout July and apparently ceased in August before the fishery for autumn-spawning herring started. Similar mortalities occurred in 1955 throughout the same areas and period, but involved both spring- and autumn-spawning stocks. In 1956 fewer herring died than in either of the two previous years and only the Chaleur Bay and Magdalen Islands areas were involved. No mortalities were reported in 1957 or subsequent years.

Leim (1955, 1956) and Sindermann (1956, 1957) investigated these mortalities and found that the dead and dying fish were infected with the fungus *Ichthyosporidium hoferi.* Sindermann (1958) showed experimentally that this pathogen caused a systemic infection which was focused in the heart and lateral line musculature of herring and which, in an acute phase, resulted in the death of the fish.

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[1] Received for publication July 25, 1962.

[2] Present address: Lothians River Purification Board, Edinburgh, Scotland.

J. Fish. Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

From observations made in 1955, 1956 and 1957, Sindermann (1958) concluded that at least half of the mature herring in the western Gulf of St. Lawrence were destroyed by this disease during the 1954–56 period. Landing statistics give some support to this conclusion. Catches for the whole Gulf area dropped from 112 million lb (50,803 metric tons) in 1954 to 77 million lb (34,927 metric tons) in 1957 and there was no indication of any decrease in fishing effort. At no time in the 10-year period before 1954 had herring landings in the Gulf of St. Lawrence been less than 100 million lb (45,360 metric tons) annually.

Studies of cod (*Gadus morhua* L.) in the Gulf of St. Lawrence provide additional evidence of the effects of the disease. Martin (1957) showed that the growth rate of cod in that area was much higher in 1955–56 than it had been during the period 1947–52. He found that 7- to 9-year-old cod were about 2 pounds (0.9 kg) heavier than formerly and concluded that "the faster growth was brought about by an increased availability of moribund herring during an epidemic of fungus disease (*Ichthyosporidium hoferi*)". Kohler (1961) recorded mean lengths of 6- to 10-year-old cod in the Gulf of St. Lawrence from 1949–59. These mean lengths not only support Martin's (1957) observations of an increase in the growth rate of cod in 1955–56 but show also that, in 1958 and 1959, there was a sharp drop in the growth rate of these fish. Kohler associates this drop in growth rate with a reduction in the availability of herring as food for cod following the epizootic.

Available data are insufficient for an analysis of the total ecological effect of the disease throughout the Gulf of St. Lawrence. Some of the results are shown, however, by the effects on herring landings and cod growth already mentioned and by comparing pre- and post-epizootic characteristics of herring stocks in a small part of the Gulf area.

The present study is based on samples of herring obtained in 1960 and 1961 from the spring- and autumn-herring fisheries in Chaleur Bay. These samples are analysed and results compared with similar data for 1947 and 1948 reported by Tibbo (1957).

MATERIALS AND METHODS

Biological studies of herring in the Chaleur Bay area of the Gulf of St. Lawrence (Fig. 1) were carried out from 1946-48 (Tibbo, 1957) and from 1952–54 (Jean, 1956). Tibbo described the size, age, growth and year-class composition of herring from commercial fisheries at Caraquet, N.B., and Bonaventure and Grande-Rivière, P.Q. He noted two distinct spawning stocks—one in the spring and the other in the autumn— but could detect only minor differences between them. Jean (1956) showed that the spring- and autumn-spawning stocks in Chaleur Bay were mixtures of fish that had been hatched in spring and autumn and hence any real differences were effectively masked.

In 1960 and 1961, samples of herring were obtained from commercial gill-net catches made at Caraquet, N.B., at the southern entrance to Chaleur Bay. The data collected by Tibbo (1957) at Caraquet in 1947 and 1948 were selected for comparison because they covered the same area and method of fishing and were available for both spring and autumn fisheries. In 1947 and 1948 the samples

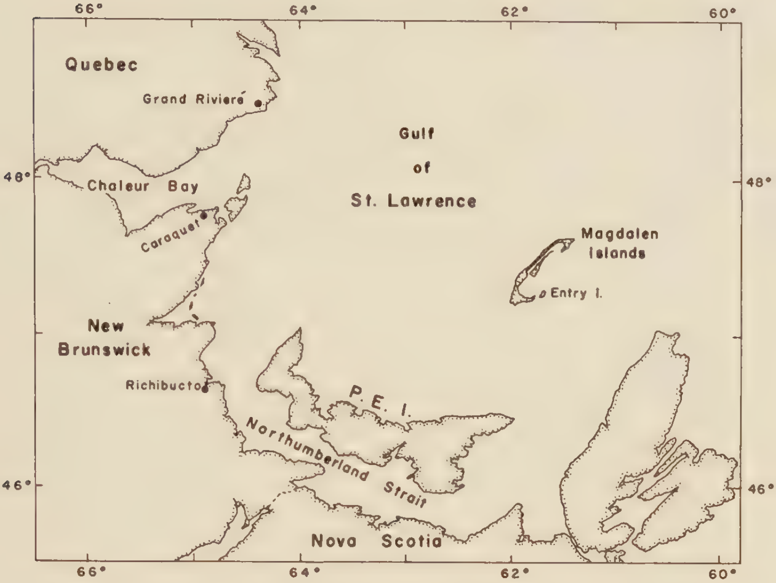

FIG. 1. Location of places and areas referred to in this report.

consisted of 330 fish from the spring, and 220 fish from the autumn fishery. In 1960 and 1961 the numbers of fish in the samples varied from 401 to 617 (Table I).

Total length of each fish was measured to the nearest half centimetre in 1947 and 1948 using a board that was offset 0.25 cm. In 1960 and 1961 measurements were made to the nearest millimetre. The total length measurement is described as the length from the tip of the closed jaw to the end of the longer lobe of the caudal fin extended straight back in line with the body. Both sets of length data were grouped by centimetres for comparison in this report. For the 1947 and 1948 data adjacent half-centimetre length groups were combined starting with an even number. The length class listed as 26 cm, for example, includes fish from 25.75 to 26.75 cm, with a mid point of 26.25. For 1960 and 1961 data, millimetre length groups were combined around the same mid-points as in 1947 and 1948. For example, the length class listed as 26 cm includes groups from 258 to 267 mm. Mean lengths tabulated, however, are true lengths which have been adjusted by the addition of 0.25 cm for all years.

Age was estimated from scales in 1947 and 1948, from scales and otoliths in 1960 and from otoliths in 1961. Age was recorded as the number of summer growth zones (including incomplete ones) on the scale or otolith. The year-class to which each fish belonged was also recorded.

For the 1960 and 1961 samples the hatching season was determined for each fish from the appearance of the otolith nucleus. Opaque, domed nuclei indicated spring hatching; hyaline, depressed nuclei indicated autumn hatching (Parrish and Sharman, 1958).

TABLE I. Length frequencies and mean lengths (in centimetres) of herring from the Caraquet area of Chaleur Bay, N.B. Methods of grouping length frequencies and calculating mean lengths are explained in text. (1947 and 1948 data from Tibbo, 1957).

Season	Frequency in successive length classes														No. of fish	Mean length
	26	27	28	29	30	31	32	33	34	35	36	37	38	39		
Spring 1947	1	12	20	23	47	79	76	40	20	12	...	...	...	...	330	31.43
Autumn 1947	...	1	2	2	8	26	57	49	24	33	14	3	...	1	220	33.22
Spring 1948	1	1	19	73	36	50	60	53	24	10	3	...	...	...	330	31.39
Autumn 1948	...	...	...	...	1	14	46	59	42	31	19	6	1	1	220	33.79
Spring 1960	...	3	26	83	57	97	118	75	29	8	3	...	...	...	499	31.43
Autumn 1960	...	...	2	19	26	47	48	52	67	58	40	24	12	6	401	33.72
Spring 1961	...	2	10	57	125	101	81	78	35	8	1	...	...	...	498	31.46
Autumn 1961	...	2	6	19	63	101	100	73	83	66	66	20	14	4	617	33.21

Collections of herring larvae were obtained from surface plankton tows nade in the Gulf of St. Lawrence during the period May to November each year ince 1951. These tows were taken primarily for studies of the abundance and istribution of lobster larvae. They were made with a plankton net (16 meshes o the inch or 6.3 meshes to the cm) which was 12 ft wide × 3 ft high × 25 ft ong (3.7 m wide × 0.9 m high × 7.6 m long) and were each of 30-minute duration.

Herring landing statistics were obtained from the Dominion Bureau of tatistics publications *Fisheries Statistics of Canada* and *Monthly Reviews of anadian Fisheries Statistics.*

RECENT HERRING LANDINGS IN CHALEUR BAY

The herring fishery in the Gulf of St. Lawrence is carried on from April to ecember with peak landings in May and August (Scattergood and Tibbo, 1959). n arbitrary separation of the spring and autumn fisheries was made by recording atches up to the end of June for the spring fishery and catches for the remainder f the year for the autumn fishery. There is justification for this separation in hat the spring fishery rarely extends beyond the middle of June and the autumn shery seldom starts before mid July.

Figure 2 gives landings of herring in the Chaleur Bay area of the Gulf of St. awrence during spring and autumn for the period 1947–61 inclusive. Annual andings varied from a high of 26.7 million lb (12,111 metric tons) in 1951 to a ow of 12.2 million lb (5534 metric tons) in 1959. From the spring fishery the argest landing was 17.9 million lb (8119 metric tons) in 1948 and the smallest

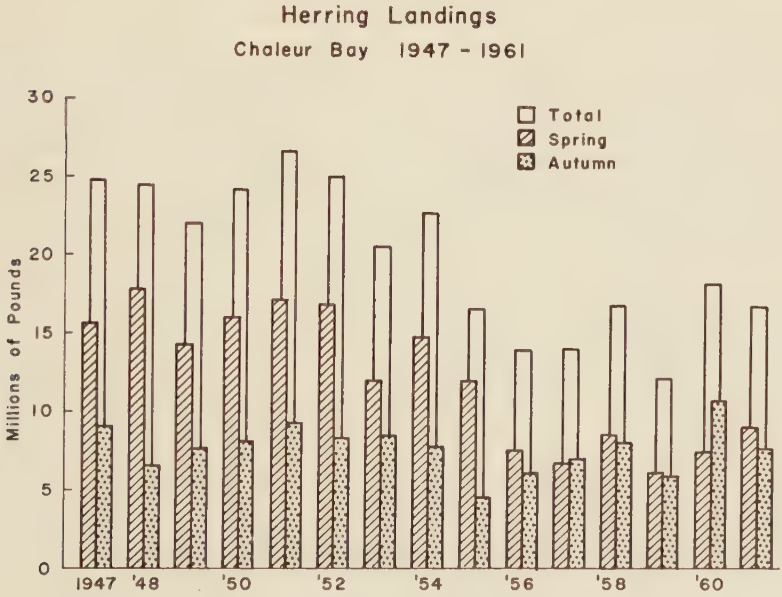

FIG. 2. Herring landings in Chaleur Bay 1947–1961.

6.3 million lb (2858 metric tons) in 1959. The largest landing from the autumn fishery was 10.8 million lb (4899 metric tons) in 1960 and the smallest 4.6 million lb (2087 metric tons) in 1955.

For the 5-year period (1950–54) before the heavy mortalities of herring occurred the average annual landing in Chaleur Bay was 23.9 million lb (10,841 metric tons). For the 5-year period (1955–59) immediately following the start of heavy mortalities the average annual landing was 14.7 million lb (6668 metric tons), a decrease of nearly 40%.

The spring fishery appears to have suffered most from the mortalities with average landings decreasing 46%, from 15.4 million lb (6985 metric tons) in 1950–54 to 8.3 million lb (3765 metric tons) in 1955–59. The autumn fishery declined 25%, from 8.5 to 6.4 million lb (3856 to 2903 metric tons) over the same period. Since 1959 there has been some evidence of recovery as average annual catches for 1960 and 1961 were 17.6 million lb (7983 metric tons) an increase of nearly 20% over catches for the 1955–59 period.

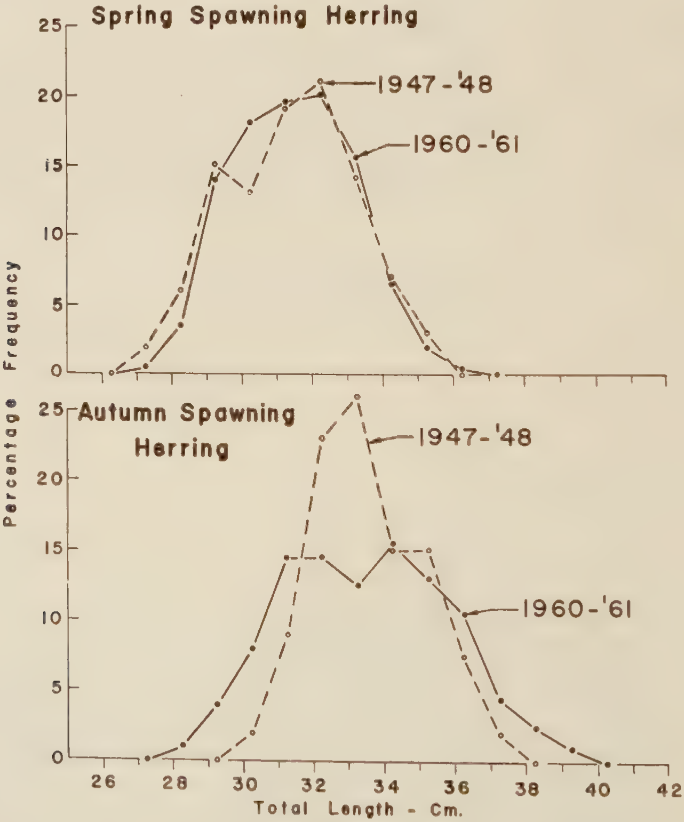

FIG. 3. Length composition of herring samples from the Chaleur Bay area in the pre- and post-epizootic periods.

SIZE AND AGE COMPOSITION

The herring fishery in Chaleur Bay is prosecuted almost exclusively with ll nets and because of their selective action (Leim *et al.*, 1957; Olsen, 1959) mples of herring obtained from commercial fishermen are undoubtedly biased. owever, there were no changes in the mesh size of gill nets used in the pre- and ɔst-epizootic periods and therefore the samples for the two periods are com- ırable.

A change in technique for age analysis from scales in 1947 and 1948 to oliths in 1960 and 1961 was considered in evaluating results. In 1960 age as estimated independently by scales and otoliths for 874 fish examined that ear. There was agreement in 57% of the age estimations by the two methods ıd the calculated mean ages differed by 0.30 years with otolith readings giving ıe higher value.

ENGTHS

Table I gives the length frequencies and mean lengths of samples of herring ken in the spring and autumn fisheries in pre- and post-epizootic periods. The ze distributions for the two periods are compared in Fig. 3. The only major fference in these results is the larger sizes of herring taken in the autumn. In ıe spring fishery small herring (less than 30 cm) were slightly more abundant the 1947 and 1948 samples than they were in those taken in 1960 and 1961. ı the autumn fishery the size range was somewhat greater for the 1960 and 1961 mples. Mean lengths for both spring and autumn fish were essentially the me before and after the epizootic.

GES

Table II shows age frequency and mean age for the spring and autumn sheries before and after the epizootic. It is obvious (see also Fig. 4) that since)47 and 1948 there has been a loss of the older fish particularly in the spring shery and a decrease in mean age for both fisheries. Such changes might be ‹pected in a new fishery or major expansion in an existing one but there is no 'idence of this in the Chaleur Bay area where herring fisheries have been prose- ıted at about the same level of intensity for a century or more.

The ages recorded for herring in 1960 and 1961 were obtained from otolith adings and the decrease in mean age in the post-epizootic period would have een greater by 0.3 years had scales been used. For all years in which samples ere taken the herring taken in the autumn fishery had a greater range of ages ıd a higher mean age.

EAR-CLASS COMPOSITION

Figure 4 shows that there are more fish 9 years of age and over present in ıtumn fisheries than in spring fisheries. Since the epizootic, there has been a ecrease in the older fish in both fisheries. This is, of course, paralleled by an crease in the proportion of younger fish.

TABLE II. Age frequencies (as year of life) and mean ages of herring from the Caraquet area of Chaleur Bay, N.B. (1947 and 1948 data from Tibbo, 1957).

Season	Age frequency																	No. of fish	Mean age
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19		
Spring 1947	...	41	55	97	43	29	11	2	4	1	1	...	...	...	...	...	...	284	6.13
Autumn 1947	...	4	10	38	85	13	18	10	6	5	9	2	2	1	...	...	1	204	7.80
Spring 1948	...	1	66	22	55	49	62	34	27	8	3	1	2	...	...	...	...	330	7.93
Autumn 1948	...	...	4	16	40	61	27	25	19	16	6	6	...	...	...	...	...	220	8.82
Spring 1960	2	49	145	195	83	5	...	...	...	...	...	...	...	...	...	...	...	479	5.67
Autumn 1960	1	28	70	81	75	42	24	35	20	10	5	3	1	...	...	...	...	395	7.19
Spring 1961	1	123	140	101	73	31	5	11	5	3	2	...	...	...	...	...	...	495	5.72
Autumn 1961	4	69	137	79	57	31	24	14	7	9	6	8	5	3	...	...	...	453	6.51

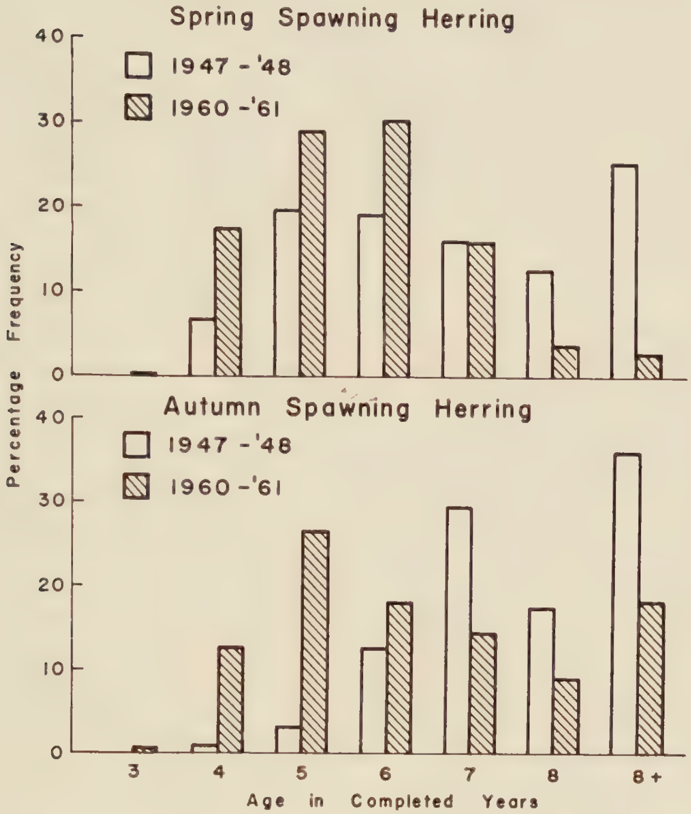

FIG. 4. Age composition of herring samples from the Chaleur Bay area in the pre- and post-epizootic periods.

ROWTH

The possibility of a change in growth rate was examined by comparing ean lengths and ages for samples and mean length for age of particular year-sses and age groups before and after the epizootic.

Table III shows these characteristics for the two periods. Mean length age 7 is used for comparison because larger numbers of that age group were tained in all years and because age 7 lies in the middle of the age range involved.

In samples from the spring fisheries, the mean length remained constant t the mean age decreased and mean length for age 7 increased. For the autumn neries the mean length fluctuated with no apparent trend. The mean age creased and the mean length for age 7 increased. Evidently the growth rate both spring and autumn herring has increased since 1947 and 1948. In all ars autumn-spawning fish are longer, older and grow faster than spring-wning fish.

TABLE III. Sample mean length and age, and mean length for age 7 herring from Chaleur Bay, N.B. (1947 and 1948 data from Tibbo, 1957).

	Spring fishery			Autumn fishery		
Year	Mean length sample	Mean age sample	Mean length age 7	Mean length sample	Mean age sample	Mean length age 7
	cm	*yr*	*cm*	*cm*	*yr*	*cm*
1947	31.43	6.13	31.40	33.22	7.80	33.30
1948	31.39	7.93		33.79	8.82	
1960	31.43	5.67	33.30	33.72	7.19	33.70
1961	31.46	5.72	32.00	33.21	6.51	34.60

PROPORTIONS OF SPRING- AND AUTUMN-HATCHED HERRING

The season in which a herring was hatched can be determined from the relative size of the 1st-growth zone on the scales (Jean, 1956) or from the appearance of the otolith nucleus (Parrish and Sharman, 1958).

Table IV gives the proportions of spring- and autumn-hatched fish in the spring and autumn fisheries for pre- and post-epizootic years. The table shows that spring- and autumn-hatched fish are present in both fisheries and that spring-hatched fish usually predominate. One exception is recorded for the autumn fishery in 1960 when the proportion of autumn-hatched herring exceeded that of spring-hatched herring.

Studies of the effects of disease on herring populations (Sindermann, 1958) and of herring landing statistics suggest a substantial reduction in the total abundance of herring in the Gulf of St. Lawrence, with the spring-spawning stocks reduced to a greater extent than the autumn-spawning stocks. This hypothesis is supported by the results shown in Table IV. In the pre-epizootic period spring-hatched herring in Chaleur Bay greatly outnumbered autumn-hatched herring, especially in the spring fishery. For the post-epizootic period the proportions were roughly equal in 1960 but in 1961 there were indications of a partial return to pre-epizootic conditions.

TABLE IV. Proportions of spring- and autumn-hatched herring in the spring and autumn fisheries in Chaleur Bay, N.B. (1952 data adapted from Jean, 1956).

	Spring fishery			Autumn fishery		
Year	No. of fish	Spring hatched	Autumn hatched	No. of fish	Spring hatched	Autumn hatched
		%	%		%	%
1952	5266	87	13	904	52	48
1960	489	58	42	198	45	55
1961	495	73	27	452	57	43

CHANGES IN ABUNDANCE OF HERRING LARVAE

Leim (1957) showed that in the western Gulf of St. Lawrence a surface rent enters Chaleur Bay from the north, circles the Bay in a counter-clockwise ection and discharges at the southern entrance. From Chaleur Bay this face current flows southward and eastward towards Prince Edward Island l divides; one part flowing along the north shore of Prince Edward Island and other through Northumberland Strait. Presumably the distribution of ring larvae in the area will be influenced by this current and the relative cess of herring spawnings in Chaleur Bay will be reflected in the abundance arvae southward and eastward from the Bay.

Since 1948 plankton collections have been made annually during the period y to November, at the western entrance to Northumberland Strait, for dies of the abundance and distribution of lobster larvae. Since 1951, slightly re than half of the 4707 tows have been examined for herring larvae. Almost of the 157,422 larvae found in the tows were less than 20 mm in length and ice recently hatched. No larvae were taken before June 15 or after September in any year and very few were taken in July. From the variation in size and nbers of larvae throughout each year it was evident that larvae caught before y 15 were the result of spring spawnings and those caught after July 15 were result of autumn spawnings.

TABLE V. Average catch of herring larvae in Northumberland Strait, N.B., 1951–61. (Numbers of tows in brackets.)

Year	Average catch per tow	
	June 16–July 15	July 16–Sept. 30
1951	74.6 (125)	0.0 (213)
1952	1897.8 (42)	0.2 (64)
1953	855.9 (35)	0.0 (68)
1954	127.4 (36)	0.2 (82)
1955	407.8 (46)	0.0 (50)
1956	31.6 (54)	0.0 (87)
1957	32.5 (73)	1.1 (77)
1958	9.1 (186)	0.0 (294)
1959	1.5 (154)	0.1 (311)
1960	11.6 (182)	0.4 (298)
1961	0.2 (175)	19.3 (293)

Table V gives the average catch of herring larvae per tow for the years i1 to 1961 inclusive. In general, the greatest numbers of larvae were taken ore July 15 in the years 1952, 1953 and 1955 in that order. Since 1952 the nbers caught before July 15 have declined irregularly to 0.2 larvae per tow 1961. Since 1956 there has been some tendency towards an increase in the nbers of larvae taken after July 15.

Comparison of the catches of larvae for periods before (1951–53) and after (1957–61) the disease epidemic of 1954–56 shows that the average catch of spring-hatched larvae decreased from 589.1 to 8.4 per tow whereas the average catch of autumn-hatched larvae increased from 0.03 to 4.6 per tow.

While there appears to be very little year-to-year relationship between commercial catches of spawning herring (the only available measure of abundance) and catches of larvae, it is perhaps significant that, over a fairly long period, changes in abundance of both follow the same trend. There has been a major decrease in spring-spawning herring and spring-hatched larvae and a modest increase especially in 1960 and 1961 in autumn-spawning herring and autumn-hatched larvae.

HYDROGRAPHY

The possibility that changes in the biology of herring resulted from abnormal hydrographic conditions was explored. Surface temperature observations have been made daily since 1930 at Entry Island, Quebec. Salinity determinations have been made from surface samples taken weekly from May to October each year since 1948 in Northumberland Strait off Richibucto, N.B. The temperatures and salinities and year-to-year variations at these stations are considered to be representative of conditions in the shallow areas of the southwestern Gulf of St. Lawrence.

During the period of the epizootic (1954–56) average temperature conditions in the area from May to October were slightly below normal but the maximum deviation from the long-term average was only 0.5°C. Salinities in the area are generally at a minimum in July. This minimum varies from year to year around a value of 27.34‰. For 1948, 1954 and 1960, i.e. before, during and after the epizootic, mid-July salinities were 27.25, 27.10 and 26.05‰ respectively.

The variations in temperature and salinity are well within the normal limits and hence the changes that occurred in the herring stocks could hardly be attributed to changes in these features of the physical environment. It should be pointed out, however, that only temperature and salinity were measured and changes in other features of the physical environment may have occurred but went unnoticed.

DISCUSSIONS AND CONCLUSIONS

Studies of the biology of herring in the Chaleur Bay area of the Gulf of St. Lawrence were carried out in 1960 and 1961 and results compared with similar data obtained in 1947 and 1948 (Tibbo, 1957). The comparison shows that in the intervening years major changes occurred in the herring stocks. These changes included a lowering of the level of abundance, a decrease in mean age, a reduction in the number of year-classes represented in commercial catches, an increase in growth rate, a decrease in the production of larvae and an increase in the relative abundance of autumn-hatched fish.

In 1957 and 1958, Olsen (1961) carried out a study of herring in Newfoundland waters. The material used included samples of herring from the west ast of Newfoundland which borders the Gulf of St. Lawrence. Olsen noted rapid decline in the herring fishery in Newfoundland over the ten-year period ior to 1957 and believed that this may have resulted from a decrease in population size. He calculated growth rates and got higher values than those found in 42–44 by Tibbo (1956).

Olsen (*op. cit.*) noted that, whereas prior to about 1950, Newfoundland rring were apparently all spring spawners, by 1958 they were spawning in actically every month of the year. The change in spawning habits was beved to have caused a change in the usual migratory pattern and general distriution of herring affecting not only availability but also abundance. Olsen sumed that growth was density-dependent and attributed his observed increase growth rate to a decrease in the level of abundance.

A fungus epizootic occurred in herring stocks throughout the Gulf of St. awrence from 1954 to 1956 and it has been concluded here that the changes in erring biology observed both by the authors in Chaleur Bay and by Olsen (1961) the west coast of Newfoundland were caused by this epizootic.

Observation of dead herring washed up on beaches and taken in the trawls groundfish draggers was ample evidence that widespread mortalities of herring curred in the Gulf of St. Lawrence during the 1954–56 period. The magnitude the mortality and its effect on the abundance of herring, however, cannot be easured and, at best can be only roughly estimated. In samples examined Sindermann (1958) the maximum incidence of disease was 78% but there were ide variations between samples and from year to year. The disease was still esent in 1957 when incidence averaged 10% but no dead herring were found at year. Undoubtedly some herring recovered from the disease but the umbers or percentages are unknown. Sindermann (1958) estimated that at ast half of the mature herring in the Gulf of St. Lawrence were destroyed uring the period 1954–56 and he considered his estimate to be conservative. hile there is no additional evidence to either confirm or refute this observation ere can be little doubt that abundance was substantially reduced. Commercial ndings of herring declined sharply following the disease outbreak with no ange in fishing effort. This could only have resulted from a decrease in the ailability of herring and while decreased availability does not necessarily dicate decreased abundance it is the only reasonable conclusion that can be ached for this particular situation.

The observed decrease in the mean age of herring and the reduction in the umber of year-classes represented in commercial catches in the post-epizootic riod can also be attributed to the effects of the disease. Assuming that the stribution of age groups at the onset of the disease was normal and that the sease was not specific for any age group it must be expected that the mean age surviving fish would remain unchanged. However, the number of recruits the commercial stocks in the post-epizootic period should be relatively higher d the end result would be a decrease in the mean age of herring taken comercially. The total disappearance of some of the older year-classes is more difficult to explain. Their level of abundance under normal conditions would be low and any further reduction in numbers due to disease would decrease the probability of finding any of the survivors in a random sample of the catch.

The increase that occurred in the growth rate of herring in the post-epizootic period may have resulted from any one of a number of factors or combination of factors. Changes in the abundance and quality of food may have occurred. Temperature changes may have resulted in greater feeding activity and hence increased growth. The fish that survived may have done so because they were in better physiological condition including a faster growth rate. However, the conclusion that is favoured here is that the change in growth rate resulted from a change in population pressure supporting the general belief that growth is density-dependent.

In spite of the fact that there has been a general failure to demonstrate a consistent relationship between the size of a spawning stock and the success of a resulting year-class or that factors affecting larval survival are equal from year to year, it is conceivable that the level of abundance of newly-hatched larvae might be closely related to the size of the parent stock. The apparent decrease in abundance of adults coincided with the observed decrease in abundance of larvae and while there can be no assurance that this was "cause and effect" such a conclusion seems reasonable under the circumstances.

The epizootic in the Gulf of St. Lawrence appeared first in the spring-spawning stocks in 1954 and continued for three years but did not appear in the autumn-spawning stocks until 1955 and lasted only two years. The effect on the autumn-spawning stocks should therefore be less extensive and this would explain their relative increase in numbers in the post-epizootic period.

Studies of sexual maturity were not included in the Chaleur Bay investigations and hence there is nothing to add here to Olsen's (1961) observations. However, the changes in spawning seasons which he observed could have resulted from a change in physiological conditions which in turn might be expected to delay development of sexual products and hence upset normal spawning habits.

The effect of disease on a marine fish population is usually included in estimating mortality rates but seldom is it accompanied by factual information. The present study provides some information on the ecological consequences of an epizootic in herring and continuing efforts to describe the sequence of events in similar situations should be encouraged.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the assistance of Messrs C. F. Monaghan, C. A. Dickson and W. H. Dougherty in the collection of samples and preparation of scales and otoliths for examination. Dr D. G. Wilder supplied the material for studies of herring larvae and Dr L. M. Lauzier supplied the temperature and salinity data. Mr P. W. G. McMullon prepared the drawings.

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Causes of Mass Mortalities of Scallops *(Placopecten magellanicus)* in the Southwestern Gulf of St. Lawrence[1]

By L. M. Dickie and J. C. Medcof

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

In 9 of the years since 1928 there have been midsummer mass mortalities of scallops in the uthwestern Gulf of St. Lawrence. There is evidence that sudden, great increases in water mperature sometimes exceeded the upper incipient lethal temperatures of scallops and that ese were directly responsible for the more devastating, sudden and widespread mortalities (up 80%).

Unusual and unexplained concentrations of predators, mainly starfish, are considered to ve been responsible for several of the slower and less spectacular mass mortalities (up to 25%). quarium tests showed that, in spite of well developed escape reactions, scallops are nevertheless ten killed by starfish.

Smaller, sudden temperature increases (too small to be lethal) and sudden decreases are mmon in the southwestern Gulf and both can cause temperature debility in scallops. Premably debility hampers escape from enemies, and magnifies effects of predation. It probably lped to produce the minor mass mortalities but so far its importance has not been assessed.

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[1] Received for publication October 4, 1961.

Fish. Res. Bd. Canada, **20**(2), 1963.
inted in Canada.

INTRODUCTION

MASS MORTALITIES of five species of commercially-important marine animals have been observed in the southwestern Gulf of St. Lawrence from time to time since about 1900. The species affected have been herring (*Clupea harengus*), and four lamellibranch molluscs—oysters (*Crassostrea virginica*), soft shell clams (*Mya arenaria*), quahaugs (*Mercenaria mercenaria*), and giant or sea scallops (*Placopecten magellanicus*). Herring mortalities resulted from sudden increases in incidence of a fungus infection (Cox, 1916b; Sindermann, 1956) and the oyster mortalities apparently resulted from a similar sort of disease (Needler and Logie, 1947; Logie, MS, 1958). Predators cause serious mortalities, particularly among small clams and quahaugs (Turner, 1948; Medcof and MacPhail, 1952; Glude, 1955; MacPhail *et al.*, 1955; Medcof and Thurber, 1958). But in some instances in the Gulf of St. Lawrence, disease was strongly suspected (Ingalls and Needler, MS, 1939 and MS, 1940). In other cases, direct effects of exceptional environmental conditions were thought responsible for a mortality among quahaugs (Cox, 1916a) and for some clam mortalities (Medcof, MS, 1950). In other instances clam and quahaug mortalities are unexplained.

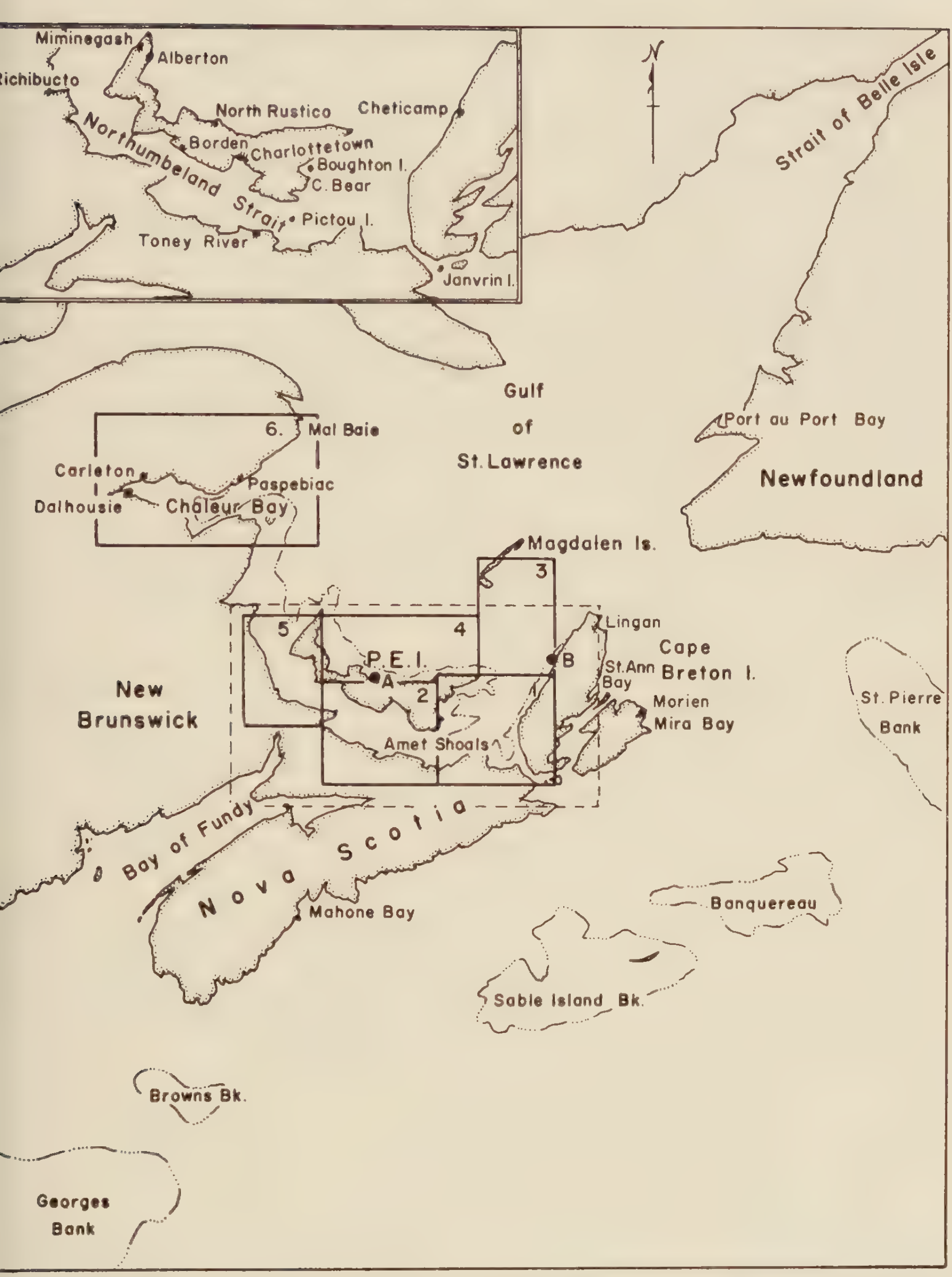
This study indicates that disease is not a significant factor in mass mortalities of scallops. The most serious and sudden mortalities occur where wind-induced oscillations in the level of the thermocline may suddenly expose scallops to water of lethally high temperature producing direct high-temperature kills. Other mortalities have been associated with unusual predator abundance. In some, the effectiveness of predator attack may occasionally have been exaggerated by temperature debility which renders scallops insensitive to the stimuli that generally provoke escape reactions.

OCCURRENCE OF MASS MORTALITIES

The giant scallop occurs along the east coast of North America from Cape Hatteras in the south to Ile-de-la-demoiselle (formerly Caribou Island) at the entrance to the Strait of Belle Isle in the north (Posgay, 1957). In the centre of this range scallops have been highly successful and have supported vigorous fisheries for about 40 years, for example, on Georges Bank, in the Bay of Fundy and in Penobscot Bay.

Toward the northern and southern limits of their range scallops have been less successful. Here, fisheries have been erratic although active for about 30 years, for example, off Long Island Sound and in the Gulf of St. Lawrence. These small fisheries are limited largely by irregular recruitment of young scallops to the fishable stocks. But in the southwestern Gulf of St. Lawrence sudden and numerous mass mortalities have placed further limits on abundance of fishable stocks.

Mass mortalities do not seem to occur generally over the scallop's range. Bourne (personal communication) reports that in 1960, "cluckers" (empty shells still attached by their hinges) composed 20% of his total catch (living scallops plus cluckers) on one part of Georges Bank. And in 1961, Posgay (personal communication) found that 30% of his catches at two other places on


Miminegash
Alberton
ichibucto
North Rustico
Cheticamp
Northumberland Strait
Borden
Charlottetown
Boughton I.
C. Bear
Pictou I.
Toney River
Janvrin I.
N
Strait of Belle Isle
Gulf of St. Lawrence
6.
Mal Baie
Carleton
Dalhousie
Paspebiac
Chaleur Bay
Port au Port Bay
Newfoundland
Magdalen Is.
3
4
5
P.E.I.
A
2
B
Lingan
Cape Breton I.
St. Ann Bay
Morien
Mira Bay
New Brunswick
Amet Shoals
St. Pierre Bank
Bay of Fundy
Nova Scotia
Mahone Bay
Banquereau
Sable Island Bk.
Browns Bk.
Georges Bank

IG. 1. Gulf of St. Lawrence region showing the six geographic zones into which scallop beds have een grouped. The 20-fathom contour indicates depths in the southern Gulf. Positions of offshore banks are indicated by the 50-fathom contour.

the Bank was made up of cluckers indicating recent heavy mortalities. N such mortalities are known to have occurred on Georges Bank during earlie years and seem not to have occurred off Nova Scotia (Dickie and Chiassor 1955; Somerville and Dickie, 1957) where conditions resemble those on George Bank. Two mass mortalities have occurred in the Bay of Fundy, one at Gran Manan Island, N.B., in 1950, which was associated with an increased abundanc of starfish (*Asterias vulgaris*) at a time of greater-than-usual abundance of smal scallops, the other in Maces Bay, N.B., in 1950, which was thought to have bee caused by drags burying and smothering scallops living on an unusually sof clay bottom. No mass mortalities are known to have occurred off Long Islan Sound or around Newfoundland in the northern Gulf.

In contrast, mass mortalities are frequent in the southwestern Gulf an possibly in two small areas in the approaches to the Gulf. These small area are Mira Bay on the southeast coast and Janvrin Island on the southwest coas of Cape Breton Island (Fig. 1). Considerable numbers of empty shells and a fe living scallops were found here during a Department of Fisheries of Canad survey made by Capt. Seymour Young in 1931 (Bruce, 1932). He conclude that mass mortalities had taken place, possibly as much as 3 years earlier. The were presumably highly localized because that same year Capt. Young found n signs of recent mortalities in neighbouring Spanish and St. Ann Bays among near-commercial concentrations of scallops.

Other observations suggest that mortalities in the approaches to the Gul do not occur frequently. A 1933 survey of the Janvrin Island region (Bruce 1934) discovered few empty shells and few living scallops. In addition, a 1951 Cape Breton survey which included Baie Bras d'Or (near Mira Bay) and Lingan Morien and St. Ann Bays discovered only a small concentration of living scallops in St. Ann Bay and no signs of mass mortalities anywhere.

In the southwestern Gulf mortalities have been common and spectacular. They have been reported in 9 of the years since 1928 and no explanation has been offered for most of them (Table I). Their wide extent and heavy toll on scallop stocks have repeatedly halted profitable fishing, making the search for an explanation of immediate practical significance. But the results of the study have general interest because many marine animals are subject to mass mortalities, although knowledge of their causes is sometimes meagre.

DETECTING AND MEASURING UNUSUAL MORTALITIES

Criteria for Detection

In scallop fishing the catches normally comprise living scallops, cluckers, separated valves, and debris. Fishermen when shucking scallops, separate the valves and throw them overboard. Thus, fishing mortality does not contribute directly to the number of cluckers on the beds. However, in all known types of natural mortality the valves remain attached for some time. In this study an unusual abundance of cluckers is accepted as evidence of high, recent, natural mortality.

in total catch of living scallops plus clappers) and bed of occurrence. Beds are identified by common name or nearest fishing port. Zones of occurrence 1 to 6 are those outlined in Fig. 1.

Line no.	Date of mortality		Year observed	Bed	Percentage mortality	Reference	Remarks
	Year	Month					
						Zone 1	
1.	1928	. . .	1929	Murray Harbour	"serious"	Young (MS, 1930a & 1930b)	"Adults began dying a year past." Good "run" of small scallops present.
2.	1928	. . .	1929	Boughton I.	75	Young (MS, 1930a & 1930b)	Smaller "run" than at Murray Harbour—enough survival to encourage fishing.
3.	1928	. . .	1932	Boughton I. Murray Hbr.	0	Bruce (1933)	Few living scallops found but signs of 1928 mortality persist.
4.	1933	July	1933	Boughton I. to Souris	90	Needler (MS, 1933)	Noted mortality in progress, complete in 2–3 weeks. No abundance of predators, all sizes sampled equally affected (>2 in. diam.).
5.	. . .	. . .	1936	Boughton I. to Souris	0	Young (MS, 1936)	No signs of recent mortality (apparently escaped in 1933).
6.	. . .	. . .	1937	Boughton I. to Souris	0	Hemphill (MS, 1937)	Few living scallops found anywhere except zone 1 (Boughton Island).
7.	. . .	. . .	1940	Boughton I.	0	Hewitt (pers. communication)	
8.	1941	Aug.	1941	Boughton I.	?	Hewitt (pers. communication)	Good fishing until August, then sudden drop in catches.
9.	1945	July	1945	Boughton I.	<20	Hewitt (pers. communication)	Slight increase in empty shells noted, catches dropped but fishing continued.
10.	1946	July-Aug.	1946	Boughton I.	30	Dickie (MS, 1951)	Empties increased from 10–30% in 2–3 weeks. No increase in predators. Sea urchins observed eating some "weak", some healthy scallops.
11.	1949	Between July 27-Oct. 15	1949	Boughton I.	0	Chiasson (MS, 1950)	Scallops abundant zones 1 and 2 in July, scarce zone 4. Mortality of 30–50% before resurvey in Oct.—no special abundance of predators.
12.	1950	Aug.	1950	Boughton I.	40	Chiasson (MS, 1951)	New mortality on Pictou I. West bed of about 40% of survivors from previous year, making total 74%, at same time as 40% on Boughton Island.

TABLE I — continued

Line no.	Date of mortality		Year observed	Bed	Percentage mortality	Reference	Remarks
	Year	Month					
13.	1950	Aug.	1951	Pictou I. East	20	Chiasson (MS, 1952)	Not observed by Chiasson in 1950 but reported by Capt. Hewitt. Checked in 1951 survey.
14.	1950	late Aug. (?)	1951	Cape Bear	57	Chiasson (MS, 1952)	Only 3% dead in 1950 survey but dead by time of resurvey June 1951.
15.	1956	. . .	1956	Boughton I.	20	Hewitt (personal communication)	Empties increased so that fishing ceased.
						Zone 2	
16.	. . .	. . .	1927	Wallace	0	Haikett (1928)	Survey showed fishing prospects in zones 4 and 5. Few living scallops elsewhere.
17.	1928	. . .	1929	Charlottetown	0	Young (MS, 1930a & 1930b)	See remarks, line 2.
18.	1928	. . .	1929	Wood I.	"heavy"	Young (MS, 1930a & 1930b)	Scallops died within a year (i.e. clean shells). Survivors healthy and fishing prospects soon.
19.	1949	Between July 27-Oct. 15	1949	Pictou I. West	50	Chiasson (MS, 1950)	See remarks, line 11.
20.	1950	Aug.	1950	Pictou I. West	40	Chiasson (MS, 1951)	See remarks, line 12.
21.	1950	. . .	1951	Pictou I. West	0	Chiasson (MS, 1952)	Total empties about same as year before (about 80%) but no signs of additional new mortality—apparently empties represented a carry-over from 1949 and 1950.
22.	. . .	. . .	1955–1958	Toney River	0	Fish. Stat. of Can. for 1955–1958 & pers. observations	New deep water bed (17–20 fath) heavily fished by industry. No signs of heavy natural mortality.
						Zone 3	
23.	1928 or 1929(?)	. . .	1932	Amherst I.	60	Zinck (MS, 1932) Bruce (1933)	Two dead to one living—"old" mortality.
24.	. . .	. . .	1953	Amherst I.	0	Somerville (pers. communication)	Incidental dragging on Le Fond George yielded a few living but no dead scallops.

Line no.	Date of mortality		Year observed	Bed	Percentage mortality	Reference	Remarks
	Year	Month					
						Zone 4	
25.	...	...	1927	Alberton	0	Halkett (1928)	See remarks, line 16.
26.	...	...	1928	Alberton	0	Anonymous (1929)	Resurvey of promising areas during summer. No mortality noted.
27.	1929	...	1929	Alberton	25	Young (MS, 1930a & 1930b)	"Buckies" (*Lunatia*) and starfish very common and eating scallops. Mortality in progress.
28.	1928	...	1932	Alberton	0	Bruce (1933)	See remarks, line 3.
29.	1933	July	1933	Rustico	80	Needler (MS, 1933)	See remarks, line 4.
30.	...	...	1936	Alberton	0	Young (MS, 1936)	No signs of recent mortality (apparently escaped in 1933).
31.	...	...	1936	Rustico	0	Young (MS, 1936)	See remarks, line 30.
32.	...	...	1937	Alberton Rustico	0	Hemphill (MS, 1937)	See remarks, line 6.
33.	1949	Between July 27–Oct. 15	1949	Alberton	0	Chiasson (MS, 1950)	See remarks, line 11.
						Zone 5	
34.	...	...	1927	Miminegash Richibucto	0	Halkett (1928)	See remarks, line 16.
35.	...	...	1928	Miminegash Richibucto	0	Anonymous (1929)	See remarks, line 26.
36.	1928	Sept.	1929	Miminegash	"heavy" = 25% (?)	Young (MS, 1930a & 1930b)	Fishermen noted scarcity in September and bodies of scallops in cod stomachs in October 1928. Notes count of 150 dead to 575 living as "heavy". Perhaps >25% at Miminegash.
37.	...	...	1936	Miminegash	0	Young (MS, 1936)	See remarks, line 5.
38.	...	...	1937	Miminegash	0	Hemphill (MS, 1937)	See remarks, line 6.
39.	1950	Aug.	1950	Miminegash	0	Chiasson (MS, 1951)	See remarks, line 12.

Table I — continued

Line no.	Date of mortality		Year observed	Bed	Percentage mortality	Reference	Remarks
	Year	Month					
40.	1950	Before July 10	1950	Richibucto A	23	Chiasson (MS, 1951)	Mortality in progress at survey time. Starfish more common in catches than scallops.
41.	1950	. . .	1950	Richibucto C	8	Chiasson (MS, 1951)	Starfish catch only 10% of that on Richibucto bed A.
42.	1950	. . .	1950	Richibucto D	0	Chiasson (MS, 1951)	Starfish rare.
43.	1951	. . .	1951	Richibucto A	5	Chiasson (MS, 1951)	Starfish only 15 to 20% as abundant as year before.
44.	. . .	. . .	1952-1958	Richibucto Miminegash	0	Fish Stat. of Can. for 1952–1958 & pers. observations	Fishing during summer of each year on several beds. Survey of Dickie and MacInnes in 1957.
						Zone 6	
45.	. . .	. . .	1921	Petit Rocher	0	Chiasson (MS, 1950)	Dept. of Fisheries files indicate fair fishing—no signs of mortality noted by biologist in charge.
46.	. . .	. . .	1923	Caraquet to Shippegan	0	Chiasson (MS, 1950)	Further survey noted good fishing prospects in eastern Chaleur Bay.
47.	. . .	. . .	1925	West Chaleur Bay	0	Chiasson (MS, 1950)	More fishing prospects on four beds in west Chaleur Bay.
48.	1933	July	1933	Carleton	"heavy"	Needler (MS, 1933)	Noted mortality in progress, complete in 2–3 weeks. No abundance of predators, all sizes sampled equally affected (>2 in. diam.) Fishery ceased.
49.	1933	. . .	. . .	Mal Baie	?	Fish. Stat. of Can. for 1933	No record of observed mortality at Mal Baie, but 8-year fishery ceased there as at Carleton.
50.	1956	. . .	1957	Miscou I.	0	Dickie and MacInnes (MS, 1958)	Size distribution of living and empties indicates a 1956 mortality. Marginal growth of empties suggests late summertime. No abundance of predators in 1957.
51.	1956	. . .	1957	Petit Rocher Paspebiac	30	Dickie and MacInnes (MS, 1958)	See remarks, line 50.

ATING AND MEASURING PAST MORTALITIES

In tank experiments conducted at the Biological Station, St. Andrews, B., in 1950, Medcof and MacPhail (unpublished data) found that when the dies of scallops are removed without injury to the hinge, the valves remain ached as cluckers for 1½ to 3 months. Dickie (1955) found that the numbers cluckers equalled 3–8% of the numbers of living scallops taken on Bay of ndy beds. From this information and the Medcof-MacPhail findings, he duced an annual natural mortality of about 10%. Posgay (personal comnication) has concluded from the low numbers of cluckers he has found that tural mortality on Georges Bank is usually low. However, Chiasson (MS, 52) found that on at least one occasion in eastern Northumberland Strait uthwestern Gulf of St. Lawrence) the period of valve attachment of a high oportion of cluckers seemed to be as long as 2 years. Thus, Chiasson's findings oport Young's (1930b) belief that the cluckers he observed in late 1929 resulted m a mortality in late 1928, and Zinck's (MS, 1932) belief that cluckers he served in 1932 resulted from a mortality in 1928 or 1929.

Uncertainty about the rate of separation of cluckers makes both dating and imates of percent mortality impossible in some cases. However, sudden reases in the relative numbers of cluckers in catches during continuous fishing erations have been accepted as evidence of mass mortalities. And even ere observations have not been made immediately after mortalities, study of ckers has been helpful in estimating times and magnitudes of mortalities. is has been possible because scallop growth rates are known (Stevenson and ckie, 1954) and because beds in the Gulf of St. Lawrence often comprise y a single year-class or are clearly dominated by a single year-class. In such ase, cluckers usually show a narrow size range with a distinct mode indicating at deaths took place almost simultaneously. The difference between modal e of cluckers and of living scallops therefore provides a measure of the time psed since the mortality. The relative numbers of cluckers and living scallops each age-class permit an estimate of the seriousness of the mortality.

Where possible, length distributions of living scallops and cluckers, and their ative numbers have been used in our studies of several recent scallop mortalities. r information on mortalities prior to 1946, we are dependent on less detailed servations by fishermen or captains engaged by the Department of Fisheries Canada for survey work. For example, Capt. Seymour Young of the Department used glossiness of shell interiors of cluckers to judge the time elapsed since rtalities. Our general observations agree with Young's (1930b) statements at this pearly lustre persists in nature for at least a year after death, but by s criterion Chiasson (personal communication) was unable to separate cent" and "year-old" empties during his 1950 studies. Young (MS, 1930a) o concluded from his observations in Mahone Bay in southern Nova Scotia at valves themselves are completely "demolished" in 3 years. This may be e in areas where shells are heavily infected with boring sponges, *Cliona tifica* or *C. celata* (Warburton, 1958a, b). However, we have concluded that lifetime of cluckers in the Gulf of St. Lawrence may occasionally be as long as 3 years and that shell decomposition takes very much longer. Like Young, we recognize occurrences of mortalities solely from the presence of large numbers of cluckers, but we concluded that we could not measure or date them accurately from this or their general appearance alone.

RECORDS OF MORTALITIES

Scallop areas in the Gulf of St. Lawrence have been grouped into six geographical zones (Fig. 1 and Table I). Reports of all Gulf scallop surveys since 1920 are summarized in Table I. Many of these are obscure manuscrips prepared for the Department of Fisheries of Canada. Others are statements from fishermen which have been filed with the Fisheries Research Board of Canada. Blanks in the table indicate that there are no records of observations and in most cases that no observations were made.

Few observations have been made on the scallop stocks in Zones 3 and 6 partly because stocks have never been abundant enough to support regular fisheries. Consequently, mortalities there may have gone undetected. Stocks in Zones 2 and 4 are sometimes abundant and fisheries have been sporadic. Mortalities may have gone unnoticed here too. However, this is less likely because there have been a number of exploratory surveys which should have detected any. Stocks in Zones 1 and 5 (eastern and western ends of Northumberland Strait) are more abundant than elsewhere in the Gulf, excepting Port au Port Bay, Newfoundland. Fishing or exploratory surveys have been carried out frequently in both these zones since 1927, but particularly in Zone 1. Thus, in these two zones the most serious mortalities have likely been detected, either while they were in progress, or a year or two later.

In the following sections, characteristics of these mortalities together with information on distribution, physiology and behaviour of scallops in relation to the regional hydrography are reviewed and possible explanations for them discussed.

CHARACTERISTICS OF MASS MORTALITIES

FREQUENCY AND INTENSITY OF OCCURRENCE

Table I shows that mass mortalities have varied in intensity from year to year and from bed to bed. The first known were reported by Young (MS, 1930a; 1930b) from his 1929 survey and appear to have been the second most widespread on record. The "serious" mortalities he noted at Miminegash (Zone 5) probably took place in September 1928. Fishermen told him that stomachs of cod caught in September and October 1928 were often filled with scallop bodies, an unusual phenomenon. He also found signs of mortality in progress off Alberton (Zone 4) during his 1929 survey. Cluckers or dying scallops made up about 25% of his catches there and he reported finding predatory animals between valves of partly-destroyed scallops. Later in 1929, he found evidence of "serious" mortalities in Zones 1 and 2. Over 75% of the catches on several beds were clean looking cluckers. He believed that scallops in Zone 1 "began dying about a year past", which he later referred to as "recently". The rtality in Zone 2 is called "very recently". Because Young's only criterion dating was clean, glossy interiors of cluckers, mortalities in the four zones ıld have taken place in either 1928 or 1929, or both. He apparently believed ıt all mortalities, except that in Zone 4, had occurred in 1928.

There are similar difficulties in dating mortalities discovered by Young Cape Beton in 1931 (Bruce, 1932) and by Zinck south of the Magdalen Islands ɔne 3) in 1932 (Bruce, 1933). In both instances, old cluckers made up 60% the catches. These mass mortalities probably occurred in 1928 or 1929.

Apparently some beds escaped the 1928 and 1929 mortalities. In November 29, Young reported a bed off Charlottetown Harbour (Zone 2) which showed unusual mortality. And in 1931 he found no signs of recent mortality on ds discovered off Cape Breton Island (Bruce, 1932).

Mortalities observed in 1933 seem to have been the most sudden, severe and lespread. In early July, fishermen reported mortalities off Boughton Island ɔne 1). In mid July, Needler (MS, 1933) reported that 75% of the catch was nposed of empty cluckers, 15% contained only meat fragments, and the naining 10% was composed of apparently healthy scallops. The larger vivors had full, nearly-ripe gonads. There were no signs of emaciation, or croparasites, and examination of formalin-preserved specimens disclosed no dence of microparasites. The shell size or straight-line measurement from bo to opposite edge of shell (Stevenson and Dickie, 1954) of the smallest llops in sample catches was about 2 inches (50 mm). All sizes seemed to ve been equally affected by the mortality.

In early August of 1933, Captain Zinck of the Department of Fisheries Canada sampled stocks he had discovered the previous year off Rustico, P.E.I. ɔne 4). He found 75% of the catches were cluckers or dying scallops (Bruce, 34). At about the same time a mortality was reported from Zone 6, in Chaleur y off Dalhousie, N.B., and Carleton, P.Q. Samples showed that at least en age-groups were affected, although 50% of a sample of the dead were 9- 10-year-olds (Stevenson, MS, 1933). There was no estimate of the pro- tion that died, but the seriousness of the mortality in the eastern part of the y is indicated by the fact that small fisheries which had operated for 12 years Mal Baie, Gaspé County, P.Q., and for 8 years off Carleton, suddenly ceased.

As in 1929, some beds escaped even this most serious and widespread of ɔwn mortalities and in reporting on his 1936 survey in Zones 4 and 5, Young S, 1936) wrote—

> "Since the scallop investigation in 1929, I have watched yearly the improvement in the condition of the scallops off the coast of Alberton. My observations of seasons past evidenced that the improvement is rapidly gaining . . . Notable beds that at one time comprised important fishing areas, before the scallops became depleted or died out in 1929, are now covered with a clean, healthy run of young scallops, ranging in size from 2½ to 4 inches measurement. There is also a large percentage of scallops ranging in size from 4 to 6 inches in these areas."

Judging from their size, all these animals were more than 3 years old and st have survived whatever conditions they were subjected to in 1933.

Mortalities in recent years have been moderately widespread but none has been as serious as that of 1933. In 1949, Chiasson (MS, 1951; MS, 1952) observed a 50% mortality on the Pictou Island West bed (Zone 2), but none on the Boughton Island bed (Zone 1) or Alberton bed (Zone 4). In 1950, he reported a further 40 to 60% mortality on the Pictou Island West bed (Zone 2) 20% mortality on the Pictou Island East bed, 60% off Cape Bear and 40% on the Boughton Island bed (all Zone 1). Also in 1950, he discovered a mortality in progress on the Richibucto bed (Zone 5). By July 10 it had destroyed 23% of the stock. Again some beds escaped the 1950 mortality. Off Miminegash (Zone 5) and on a small unnamed bed near the Richibucto bed, he found that cluckers made up less than 8% of the catch. In 1956, Dickie and MacInnes (MS, 1958) report mortalities of 20 to 30% in Chaleur Bay (Zone 6) and Hewitt (personal communication) also reported minor mortalities on the Boughton Island bed (Zone 1).

Thus it appears that mortalities on any one bed usually occur at irregular intervals of several years. But in some cases there is a suggestion that they occurred in successive years. For example, serious mortalities may have taken place in both 1928 and 1929, or in only one year. Again, following the widespread mortality in 1933, fishing stopped and there were few observations in 1934. Similarly, following the small 1941 mortality on the Boughton Island bed, commercial landings dropped to a low level. There were few reports of any kind in 1942 and we cannot be sure that survivors were not subjected to a second mortality that year.

In other cases they certainly occurred on the same bed in consecutive years. Dickie (MS, 1951) in studying the 1946 Boughton Island mortality was informed by fishermen that a light mortality had also occurred there in 1945. Similarly, Chiasson (MS, 1952) concluded that the 75% empty shells observed in 1950 on the Pictou Island West bed was the result of mortalities in both 1949 and 1950. We know of no case where it has occurred in three successive years.

This history of observed mortalities illustrates their erratic geographic and temporal occurrences and their great variety in intensity.

SEASON OF OCCURRENCE

Although the mortalities are sporadic in their year-to-year occurrence, they are consistent in that they occur only in summer or early autumn, from July to September. Except for the 1928 Miminegash mortality, all those observed in actual progress took place in July and August. The season of occurrence of those not observed while in progress can be surmised only, but there is no evidence to conflict with our assumption that they occurred in this same short period.

DEPTH DISTRIBUTION

Information on the depth of water in which mortalities have occurred was not systematically recorded until recent years. The first part of Table II shows the relative number of cluckers and living scallops taken in 1951 from several different areas in Northumberland Strait (Zones 1 and 2) by Dickie (MS, 1952) using a small flounder trawl ($\frac{3}{4}$ No. 35 Yankee otter trawl). The second part of

BLE II. Relative numbers of cluckers (empty attached valves) and living scallops taken at different depths in Northumberland Strait in 1951 in a flounder trawl and scallop drag.

		Flounder trawl			Scallop drag		
			Cluckers			Cluckers	
Place	Depth	Hauls	Living	Cluckers	Hauls	Living	Cluckers
	m	*no.*	*no.*	%	*no.*	*no.*	%
pe Bear	17	...	...	...	1	302/240	56
pe Bear	22	...	...	...	2	429/261	62
ctou I. West	22–27	1	5/0	100	7	4864/1046	82
ctou I. East	31–33	2	0/13	0	16	1351/5104	21
orge Bay	31	1	15/16	48	...	...	...
orge Bay	33	1	24/39	38	...	...	...
pe Bear	33	...	...	...	2	130/147	47
eep water off Boughton I.	33–38	4	1/17	6	...	...	...
pe Bear	37	1	0/2	0	...	...	...
net Shoals to Indian Rocks	37	1	12/189	6	...	...	...
net Shoals to Indian Rocks	42	1	0/300	0	...	...	...

e table shows catches made at about the same time by Chiasson (MS, 1952) sing scallop drags. Although a flounder trawl is not efficient in taking scallops, e proportions of cluckers in its catches were roughly the same as in catches by allop drags in those areas where both were used. Assuming that the relative lectivity of the two types of gear in taking scallops and cluckers was the same, e pooled data show that there was an abrupt decrease in the proportion of uckers below 33 metres.

Dickie and MacInnes (MS, 1958) noted a similar relationship in Chaleur ay where scallop concentrations are in shallower water than farther south. long the northern shore of the Bay off Paspebiac, they found scallops in depths nging from 11–29 metres (6–16 fathoms) with highest concentrations between 4 and 20 metres (8 and 11 fathoms). In shallow parts of the range (11–18 etres or 6–10 fathoms) cluckers made up about 30% of the catch but in deeper ater (more than 18 metres or 10 fathoms) they were rare.

It would appear that low mortalities are usually found in deep water. t the same time high mortalities may be found in the nearby shallow or intermediate depths.

ZE SELECTION

Information on what beds were affected and on how fast they recovered somewhat obscured by conflicting reports of how susceptibility may vary with ze of scallops. Needler (MS, 1933) noted no size selection down to 2 inches, the nallest scallop in his samples. However, Dickie (MS, 1951) sampling with a nall-mesh dredge in 1946 found relatively fewer cluckers among small scallops ess than 2½ inches) than among large. He postulated better survival of the young but realized that his observations could also have been explained by either lower catchability or a higher rate of separation of the smaller cluckers.

Dickie's postulation receives some support from subsequent observations By late 1949 there was a successful fishery on the Boughton Island bed following the 1946 mortality. This fishery persisted for several years. In 1949, the moda size of the commercially available population was $3\frac{1}{4}$ inches (80 mm). According to growth information (Dickie, MS, 1951; Chiasson, MS, 1952), these animals were at least 5 years old in 1949; hence, 2 years old and $1\frac{1}{4}$–$1\frac{3}{4}$ inches (30–45 mm) shell diameter in 1946. This is the size which Dickie believed survived the 1946 mortality of larger scallops. Observations by Chiasson (MS, 1950; MS, 1951) suggest a similar phenomenon on the Pictou Island West bed. Large cluckers from the 1949 mortality made up 30 to 50% of his catches with commercial drags. Apparently a further 40% mortality occurred there the next year because in 1950 cluckers constituted 75% of the catch. In spite of this, when Chiasson towed with a small-mesh drag in 1951 (Chiasson, MS, 1952), 75% of his live catch was composed of 2-year-old scallops ($1\frac{1}{2}$ inches = 40 mm). These must have set in 1949 and survived the 1950 mortality.

From this information, it is certain that appreciable numbers of 1- and 2-year-old scallops have survived mass mortality—in some cases enough to support a fishery when they reached 5 years of age. However, this may still not justify the conclusion that there is a size-selection in mass mortalities Mortality rates are commonly believed to be higher among very young than among adult or middle-aged animals. If this is true, then any new competing causes of mortality (e.g. mass mortalities that are not selective for size) might appear to have less effect on survival of young than older year-classes of scallops Our information suggests that the annual natural mortality rate among scallops 5 years and older is about 10% (Dickie, 1955). Additional sources of mortality of the magnitude known in mass mortality (two to eight times normal mortality rates) would therefore be likely to reduce the stock of these ages to an abnormally low level and seriously affect fisheries depending on them. We have no estimate of the natural mortality of young scallops but if it were normally high, mass mortalities of the order observed would be relatively less important than among older animals and might have little effect on the relative strength of a year-class when it enters the fishery 4 or 5 years later.

Without further information, we cannot say whether there is a size-selection during mass mortalities or not. We may conclude only that the rate of recovery of a bed is highly variable and depends on the presence or absence of strong year-classes of juveniles to provide recruits. These recruits may be produced in the years during or immediately preceding mortalities of adults and survive to provide substantial fisheries in later years.

Rate of Mortality and Association with Predators

Mass mortalities have occurred when predators were abundant and when they were not. Those when predators were abundant have usually been gradual and relatively light. An example is the 25% mortality in 1929 on Alberton beds (Zone 4) noted by Young (MS, 1930a; 1930b) as associated with unusua oundance of predators (Table I). He considered starfish (*Asterias vulgaris*) id "buckies" (*Lunatia heros*) to be the worst. Another example is the 23% ortality on Richibucto bed in 1950 (Chiasson, MS, 1951). This probably took ace between late June and early August and was apparently in progress during hiasson's July sampling. It was associated with an unusual abundance of arfish (*A. vulgaris*).

On the other hand, mortalities when predators were not so abundant have ten been sudden and heavy. An example is the 90% mortality in Zone 1 ported by Needler (MS, 1933) who found no evidence of predation or macro- ırasites. Similarly, Dickie (MS, 1951) noted no unusual abundance of predators the moderate but sudden 1946 mortality in Zone 1. Chiasson (MS, 1951; S, 1952) reported a number of explosive mortalities which also fit here. They ere in Zones 1 and 2 and seem to have occurred within periods of only 2 or 3 eeks without unusual abundance of predators, although Chiasson did find veral gaping, half-eaten scallops with small sea urchins (*Strongylocentrotus oebachiensis*) (scavengers?) inside.

FFECTS ON SURVIVORS

Mortalities have taken place both before and after spawning and specimens amined closely during a mortality (Needler, MS, 1933; Dickie, MS, 1951; id Chiasson, MS, 1951) showed no signs of emaciation. In mortalities which curred before spawning, survivors seemed healthy and in excellent condition. urthermore, shells of survivors showed no shock-marks from growth interruption tevenson and Dickie, 1954). From this it is deduced that survivors of mor- lities suffer little from their experience.

ATE OF RECOVERY OF STOCKS

Scallop stocks that have suffered mass mortalities usually recover rapidly. 1932, Bruce (1933) reported that Zinck found large numbers of small allops ($2\frac{1}{2}$ to 5 inches) on the Boughton Island bed (Zone 1) indicating a rapid covery from the 1928 or 1929 mortality. Young (MS, 1936) also observed pid recovery on the Alberton bed (Zone 4) after 1929. Although Chiasson AS, 1952) reported mortalities on Pictou Island West (Zone 2), Pictou Island ast and Boughton Island (Zone 1) beds in 1950, recovery seems to have been pid.

Although scallops can swim, their swimming powers are limited and tagging, owth studies and general observations show little or no migration of the adults om bed to bed. Rapid recoveries cannot be attributed to migrations of allops from unaffected areas. Recovery of a bed must therefore be attributed holly to successful development of scallops that settled there as larvae and to e presence of adult survivors of mortalities.

EXPLANATION OF MORTALITIES

Various explanations have been offered for scallop mortalities—starvation, eakness in spawning season, senescence, disease, predators, and hydrographic onditions. The first three have little plausibility. The others merit full onsideration.

STARVATION

Dead scallops are often plump-meated and survivors healthy with full gonads. This eliminates starvation as a likely cause of mortality.

WEAKNESS IN SPAWNING SEASON

Scallops held in tanks throughout the year, observed and handled during the spawning season and at other times, have never shown differences in their ability to respond to external stimuli at spawning time. Furthermore, mortalities have taken place before and after the regular spawning time, late August or September (Dickie, 1955; Posgay, 1958). Thus, mortalities and spawning do not seem directly related.

SENESCENCE

Captain Seymour Young, who first observed mortalities, proposed that deaths of scallops from senescence created unfavourable conditions that killed the young and initiated mortalities. However, recent observations have revealed mortalities on beds populated by only young scallops. Furthermore, in early stages of sudden mortalities there has been little evidence of size and age selection among half-grown and old scallops. In addition, the occurrence of mortalities on the same bed in consecutive years cannot be explained by the senescence hypothesis.

DISEASE

To date there has been little study of the microflora and microfauna of scallops. Recently, Dr Marshall Laird (personal communication) found a ciliate (*Trichodina*) in healthy scallops from Passamaquoddy Bay and Mr P. J. Downer (personal communication) found *Hexamita* in a dead scallop in one of this Station's aquaria. However, Needler (MS, 1933) found no signs of infestation of living and dead specimens during the 1933 mortality and Dr H. B. Fantham (personal communication) of McGill University found nothing resembling a disease organism in Needler's preserved specimens.

Nevertheless, Sindermann (personal communication) has suggested that scallop mortalities may be caused by *Ichthyosporidium*—the fungus responsible for "pepper-spot" disease of herring (Sindermann and Scattergood, 1954; Sindermann, 1956).

Mortalities of herring and scallops are similar in their sporadic occurrence, in their simultaneous appearance in different districts and in their abrupt ending. However, the characteristic signs of *Ichthyosporidium* infection have not been found in scallops anywhere. Furthermore, *Ichthyosporidium* has been epidemic among herring in the Gulf of St. Lawrence where scallop mortalities often occur, and among herring in the Bay of Fundy and Gulf of Maine (Scattergood, 1948) where scallop mortalities seldom occur. Any similarity in epidemiology is therefore probably fortuitous, especially in view of the very different behaviour of the animals, herring being wide-ranging migrants while scallops are sedentary. The similar histories of epidemics in the Gulf therefore offer no grounds for assuming identity of causative mechanisms for mortalities in the two species.

It has also been suggested that scallop mortalities are caused by the organism sponsible for the disease of oysters which began in 1915 in Malpeque Bay, E.I., and has since spread to most oyster areas in the Maritime provinces eedler and Logie, 1947). This organism has not been isolated but Logie IS, 1958) has studied its etiology and epidemiology. It spreads from foci of fection and recovery of affected oyster stocks is very slow.

One might expect that a scallop disease would more likely resemble an ster disease than a herring disease because of the closer relationship and milarity of habits of the molluscs. But dying scallops do not show the symptoms scribed by Needler and Logie and the pattern of scallop mortalities is quite fferent from that in oysters. Instead of spreading from a focal point they often pear in widely-separated localities, skip over intervening areas, and show much riety in intensity. Besides this, most are over-with in a single year and re- very from them is rapid—a pattern very different from that of an oyster ortality. Other disease organisms might be responsible for scallop mortalities ut pathological symptoms frequently associated with diseases, such as naciation, retardation of growth, or effects on seasonal gonad maturation ay and Chandler, 1955) have not been observed among scallops during or ter mass mortalities. These characteristics and the possible superior resistance young point to some causes other than disease for mass mortalities of scallops.

REDATORS

There is no doubt that predators have destroyed scallops in the Gulf of . Lawrence in varying intensities from time to time, and that they have been ainly responsible for some mass mortalities. Olsen (1955) reached a similar nclusion from his Tasmanian studies. Our best evidence was reported by hiasson (MS, 1951). In 1950, he discovered the well-stocked, 3-square-mile ichibucto bed (Zone 5). The size of 90% of the living scallops ranged from –80 mm (2–3¼ inches) with a mode at 70 mm (2¾ inches). About 23% of e catch was cluckers and their size distribution was almost identical with that the living animals. Starfish were unusually abundant—as many as 1,500 ere caught in a single haul. A few starfish were found inside scallops feeding partly-destroyed bodies. The bodies of both the dead and living scallops oked normal.

About 3 miles from Richibucto bed, Chiasson found a smaller bed, three arters of a square mile in area, with similar densities of scallops. About 92% the catch showed the same size range as the stock on the larger bed. The maining 8% were larger scallops. The "catch" of starfish was only 10% and e frequency of cluckers only 8% of that on the Richibucto bed. Twenty-six uls were made on two other small nearby beds. There the size range of scallops ken was 62–128 mm (2½–5 inches) and comprised four distinct modes of about ual strength. Starfish were rare and cluckers comprised less than 1% of the tch.

In 1951 the Richibucto bed was resurveyed and a typical haul contained ly 200–300 starfish. Cluckers now made up about 5% of catches. But both uckers and living scallops were of the same age group as that sampled in 1950.

In July 1952, Chiasson (unpublished data) conducted a laboratory experiment to elucidate some of these field observations. He placed 71 starfish (*Asterias vulgaris*) of various sizes and 100 scallops of various sizes in a tank with a bottom area of 75 square feet. His observations agreed with those of Galtsoff and Loosanoff (1939), Smith (1940), and Loosanoff and Shipley (1947) that starfish are unable to detect the presence of food from a distance.

He was therefore unable to explain why the starfish were so abundant on the Richibucto bed as compared with neighbouring beds in 1950, or why the abundance dropped in 1951. Possibly they were moved about by water currents in the manner described by Loosanoff at the 1959 meeting of the National Shellfisheries Association. He quoted divers' reports of starfish arching their arms so as to be rolled along the bottom by currents. Presumably they could stop when they came into contact with potential food. The relatively large Richibucto bed bearing a relatively dense stock of uniform-sized scallops might then have been an ideal area for concentrating the starfish.

The smaller starfish concentrations on neighbouring beds may be accounted for in part by less favourable tidal currents or the smaller areas of the beds or possibly the wider size distribution of the scallops. A starfish must be at least 1½ times the diameter of an oyster to kill it (Needler, 1941). If a similar relationship holds for starfish and scallops, the 70 mm scallops on the Richibucto bed should have been ideal food for the 130 mm starfish found there in 1950. Sizes of scallops on neighbouring beds would have been less suitable as starfish food. Unfortunately data on relative sizes of starfish and scallops in 1951 were lost in an explosion on the survey vessel!

Since Chiasson's laboratory test showed that the starfish ate approximately 20% of the scallops in 15 days (0.02 scallops per starfish per day) there is little doubt that the unusual abundance of predators in 1950 was responsible for the 23% scallop mortality on Richibucto bed. The lower mortalities on small neighbouring beds in 1950 and on the Richibucto bed in 1951 are explained by the lower starfish abundance.

There are other cases where an unusual abundance of predators appears to have been responsible for high scallop mortalities. In the 1929 mortality off Alberton, P.E.I. (Zone 4), Young (MS, 1930a; 1930b) reported that starfish and *Lunatia heros* were especially abundant and frequently found between the valves of half-eaten scallops. The *Lunatia* appeared to have bored into the adductor muscles. As on the Richibucto bed, cluckers made up about 25% of the catches.

In both the 1950 and 1929 cases, predators were abundant and seemed to have been the immediate agents of scallop destruction. But even then mortalities were low compared with some other mass mortalities.

Moderate or high mortalities have been observed without unusual abundance of predators. The 30%, 1946 mortality on Boughton Island bed (Zone 1), (Dickie, MS, 1951) is a good example. Predators were scarce although Dickie did observe a few sea urchins (*Strongylocentrotus droebachiensis*) eating scallops with mantle edges shrivelled and fallen away from the shell. The decayed condition of the scallop bodies indicated that death had occurred before invasion by e predator (scavenger). The few other scallops he observed under attack were althy and alive. Predation is a still less acceptable explanation for the 75%, 28 and the 90%, 1933 mortalities off Boughton Island (Table I). Some other ctor or factors must have been responsible.

YDROGRAPHIC CONDITIONS

Huntsman (1918) recognized a relation between depth distribution of certain arine animals and hydrographic conditions in the southwestern Gulf of St. wrence. There he found adults of several species of molluscs and echinoderms stricted to 20–30 fathoms. In the Bay of Fundy he found these same forms ere distributed from the intertidal zone to 30 fathoms. Several of these species ve pelagic larvae and in the Gulf he found the juvenile stages of these through- t the vertical range.

Bay of Fundy waters are thoroughly mixed by tidal action and have a rela- vely uniform temperature from top to bottom, even in summer. In the southern ulf, on the other hand, animals at intermediate depths are in summer exposed ternately to very warm and very cold water because of oscillations in the level a sharp thermocline separating the warm surface and cold bottom water. untsman attributed the differential distribution of adults and young in the ulf to the greater ability of the juveniles to survive high temperatures or sudden mperature changes. Later, in personal communications with Dr Needler, suggested that oscillation of the thermocline may have been responsible for e 1933 mortalities of scallops in the southwestern Gulf of St. Lawrence and haleur Bay.

Since the 1930's, much information has been gathered on hydrography of e southwestern Gulf of St. Lawrence. In addition, recent knowledge of the allop's ability to tolerate hydrographic changes affords a good basis for judging e aptness of Huntsman's suggestion.

TOLERANCE OF SCALLOPS TO TEMPERATURE CHANGES

HE LETHAL TEMPERATURE CONCEPT

There have been many studies of distribution of marine animals in relation the temperature of their environment (Huntsman and Sparks, 1924; Gowanlock d Hayes, 1927; Henderson, 1929; Broekhuysen, 1940; Evans, 1948; Southward, 58). These have demonstrated parallels between the highest temperatures pected in the environment and the temperature at which the animals die lethal temperature") when they are subjected to increases of 1°C every 5 inutes. They have also shown that the lethal temperatures so determined are likely to occur in the natural environment. In the case of the scallop, for stance, Stevenson (MS, 1936) determined the lethal temperature at 30.6°C. his is, of course, far above temperatures likely to be experienced by scallops our coast.

With this concept of lethal temperatures, it is understandable that few thors have reported mass mortalities of marine animals attributable to high mperatures. The best known is that associated with El Niño, the warm uatorial counter-current, off the coast of Peru (Brongersma-Sanders, 1957).

However, knowledge of temperature as a lethal environmental factor has grown in recent years through the work of Fry (1947) and his associates. They have shown that sudden, frequent and great temperature changes do not kill animals as long as these changes are within the "zone of thermal tolerance" which characterizes their species. But above this there is for each species a series of threshold temperatures, the "incipient upper lethal temperatures", corresponding to the temperatures at which they have been acclimated (Fig. 2, solid line). Animals which have experienced the same recent thermal history behave similarly when exposed to temperatures above their upper lethal and they show a characteristic median survival time. The highest or "ultimate" (Fry, 1947) incipient upper lethal temperature is reached when the upper lethal corresponds with the acclimation temperature. The upper boundaries of a zone of thermal tolerance may therefore be defined by the area under the line describing the relation between upper lethal and acclimation temperature.

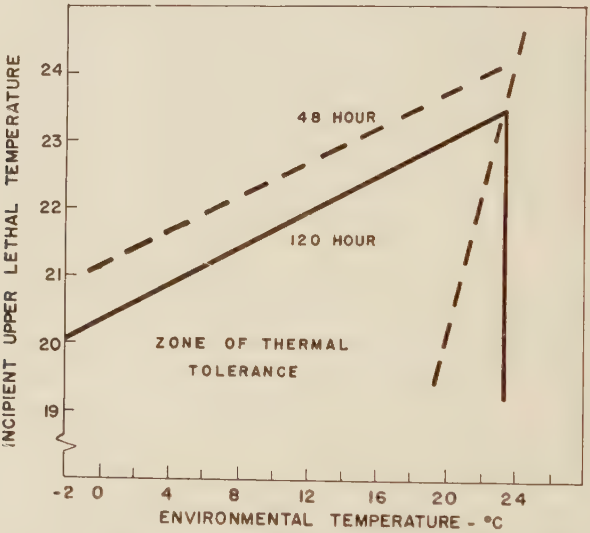


FIG. 2. Relationship between upper incipient lethal temperatures (temperature causing 50% mortality: upper line in 48 hours, lower line in 120 hours) and temperatures to which scallops are acclimated during seasonal changes in environment.

In the light of this recent work it appears that lethal temperatures determined by the old gradual heating method provide a useful measure of relative sensitivity of different species to high temperature but beyond this they have little meaning for interpreting field observations. In contrast, the considerably lower incipient upper lethal temperatures determined by Fry's method do have meaning when applied to field conditions and can be used with confidence in our present study. Accordingly, scallop mortalities attributable to direct effects of high temperature may be expected, and indeed seem to occur, when sustained vironmental temperatures rise beyond the zone of thermal tolerance. These nperatures have been determined (Dickie, 1958) and found to be lower than e lethal temperature reported by Stevenson.

Experiments show that high temperatures kill scallops but they also show at less extreme temperatures are debilitating (interfere with normal activity) d might hasten death from other causes; i.e. they may be indirectly rather than ectly lethal. For example, debility from temperature fluctuations might be pected to interfere with their escape reactions when attacked by predators.

MPERATURES LETHAL TO SCALLOPS

Dickie's definition (1958) of seasonal upper temperature tolerance limits of allops is summarized in Fig. 2. It shows the incipient upper lethal temperatures scallops that have been living at (i.e. were *seasonally* acclimated to) different vironmental water temperatures. Sea water freezes at about −2°C. If allops that have been living at this temperature are suddenly exposed to a nperature of 20°C, 50% of them will be dead after 120 hours (Fig. 2). The asonal upper lethal temperature rises 0.14°C for each 1.0°C rise in temperature which the animals have been acclimated during seasonal change. So scallops ich have been living at 5°C have an upper lethal of 21°C, those living at 10°C ve an upper lethal of 21.7°C, and those living at 15°C have an upper lethal of .4°C. The ultimate (in this case "maximum", McLeese, 1956) upper lethal curs at a temperature of 23.5°C.

When the temperatures to which acclimated scallops are suddenly exposed e correspondingly higher than those just mentioned, the 50% mortality is ected in a shorter time. Thus, 50% mortality occurs in 48 hours (Fig. 2, oken line) at temperatures uniformly 0.8°C higher than those which kill them 120 hours.

Conversely, higher or lower temperatures produce a higher or lower per- ntage mortality in a given time. It was found, for instance, that 75 and 25% ortalities occurred in 48 hours at temperatures respectively about 0.3°C above d below those which effect a 50% mortality. Thus, the likelihood of occurrence a scallop mortality following a given temperature change, and the extent of y mortality that may occur, depend on the animal's temperature experience e. seasonal acclimation state) previous to the change and the length of time to ich the animals are exposed to the high temperature.

Dickie's (1958) review of the experimental work of Johannes (MS, 1957) led to show that small scallops of 50 to 60 mm (2 to 2$\frac{1}{3}$ inches) are more resistant high temperature than larger animals. However, Huntsman (1918) reports at the very young of both starfish and urchins are more resistant to high nperature than adults. Smith (1940) confirmed this for starfish when he und that 1–2-mm specimens could tolerate 27.5°C while 90-mm animals died 23°C. Kerswill (MS, 1941) has shown a similar greater tolerance of high nperatures by young (1–2 mm) quahaugs (*Mercenaria mercenaria*) in Bideford ver, P.E.I. Similar temperature tolerance results have been recorded among es by Day (1885), Huntsman and Sparks (1924), Fry *et al.* (1946), Brett 44) and Hart (1952). It seems reasonable, therefore, to expect very young scallops to be more resistant to high temperature than old. This was suggested by Dickie (MS, 1951) and in our section on Size Selection. The uncertainty about temperature resistance of young and their superior survival in mass mortalities has still to be clarified by field and laboratory observations.

Thus, direct temperature kills are to be expected among scallops of most ages when temperatures rise to levels of 20 to 23.5°C. Their actual occurrence and severity under these conditions will depend on the immediate past temperature experience of the stock and the length of its exposure to the increased temperature.

TEMPERATURES DEBILITATING TO SCALLOPS

Experiments show that temperature kills are caused only by great upward temperature changes that may obtain for several hours or days. They also show that after any substantial temperature change, upward or downward, within the zone of thermal tolerance, scallops exhibit symptoms of shock or debility. Dickie (1958) reported that after raising the temperature by about 10°C or to any temperature above about 20°C and maintaining it, his scallops were unable to close their valves for periods of 24–36 hours and produced copious mucus secretions. He also reported that when he suddenly lowered the temperature by as little as 4–7°C and then held it constant, scallops were unable to close their valves for periods of up to 40 days.

These reactions have been little explored in scallops but it is pertinent to mention that for lobsters McLeese and Wilder (1958) have described a thermal "zone of activity" and a "zone of inactivity", both of which lie within the zone of thermal tolerance. Something similar seems to exist for scallops because temperature changes can induce debility without killing them. In nature this must produce many intricate co-actions because predators undoubtedly take advantage of scallops suffering temperature debility from upward or downward temperature changes that lie within the zone of thermal tolerance. We have made several observations which indicate how these may come into play.

Several species of scallops avoid starfish by "jumping back" or swimming after the starfish touches them. Uexküll (1912) observed a rapid and strong "flight" reaction by *Pecten maximus* when touched by *Marthasterias glacialis*, and ascribed it to a chemical rather than a simply tactile stimulus. Lecomte (1953) working with *Pecten jacobeus* confirmed Uexküll's observations with *M. glacialis*. But he found that his scallops reacted much less sensitively to four other species of starfish. The scallop's reaction to at least one starfish was similar to its response to mechanical prodding.

Our observations in tanks agree with those of Lecomte. *Placopecten* almost always reacts vigorously to *Asterias vulgaris* and usually swims away from contact. In contrast, our scallops seem undisturbed by contact with the starfish, *Crossaster papposus* which in its turn appears usually to avoid scallops.

Chiasson (unpublished data) did not observe flight reactions of scallops (*Placopecten*) during his daily observations in 1952. Possibly this was because his tanks were crowded and chance encounters between scallops and starfish so frequent that the scallops were perpetually tired and did not react conspicuously. Olsen (1955) claims that they do tire and we agree. We have often erved that sharp tapping on the wall of an aquarium induces swimming by st scallops in it. If the tapping be repeated immediately after the scallops le, fewer of them react, and after a fourth or fifth repetition neither tapping prodding elicit the response. Reactions of normal strength and frequency be induced again after a rest period of 3 or 4 hours. Reactions to starfish seem to weaken if repeated frequently.

Chiasson found that starfish ate scallops with broken or injured shells ore they ate uninjured scallops. He also showed that starfish encounter their y by random wandering. From his results and our observations we conclude t the uninjured scallops in his tanks were actually avoiding capture to a ited extent. We may further conclude that the susceptibility of scallops to dation is increased by factors which inhibit their normal reactions—for mple, substantial temperature fluctuations up or down.

Temperature change, up or down, probably impairs normal activity of the lop's predators just as it does that of scallops. In extreme cases, predator prey may both be killed by lethally high temperatures. Smith (1940) gests that the incipient upper lethal temperature for starfish (*Asterias vulgaris*) lose to that which has been worked out recently for scallops. He interpreted fish mortalities that were observed in Bideford River, P.E.I., as temperature s induced by water temperatures above 23°C. His work on the zone of thermal rance of starfish should be reviewed and we should also explore their thermal e of activity.

HYDROGRAPHY OF THE SOUTHWESTERN GULF OF ST. LAWRENCE

Hydrography of the southern Gulf has been described by Lauzier *et al.*, 57) and by Lauzier (1957, 1958). The salinity of the water within the upper rs (0–30 m) varies from 26 to 31‰ depending on season. Changes of this er are not significant in the survival of scallops (Dickie, 1958). We have refore focused attention on temperature characteristics that might be signi- nt.

In winter the water is cold and isothermal to depths beyond 23 m (13 fath), average depth of scallop beds. But in spring a warm surface layer appears, arated by a thermocline from the deep layers that continue cold. By late nmer its depth often approximates 23 m. But it may be as shallow as 10 m ath) (Zone 5, August 1950) and as deep as 30 m (17 fath) (Zone 3, July 1950). Lauzier (1952) has also shown that off North Rustico, P.E.I. (Zone 4) off Cheticamp, N.S. (Zone 3), summer winds frequently produce giant erings of the thermocline. And these are responsible for sudden temperature nges which extend into Northumberland Strait where many scallop beds are ted and where scallop mortalities occur in summer. The beds are at different ths. Some are at intermediate depths—about the depth of the late summer mocline (23 m). Others are in deeper water and still others are in shallower er and well above the level of the summer thermocline. It is instructive to mine the variety of hydrographic conditions that obtain at the surface and hese depths in the various zones.

The information is sparse. From 1945 to 1951 records for the various zones were irregular as regards both position and timing. But in 1951 regular daily observations were begun off Borden, P.E.I. (between Zones 2 and 5) and the irregular observations in various zones were continued as occasion permitted.

Table III summarizes some of the irregularly recorded surface and 23 m temperature maxima for July and August in various years. These are listed by zones for comparison along with some of the regularly observed Borden observations which appear to be roughly representative of all zones.

TABLE III. Highest recorded July and August offshore water temperatures (surface and 23 m) at various stations in the five zones of the Gulf of St. Lawrence for the years 1945 to 1957 compared with surface temperatures at the regular Borden, P.E.I., hydrographic station (Zone 2). Unbracketed Borden temperatures were taken the same day as those in Zone 1; bracketed are maximum temperatures for that month.

Date		Borden (surface only)	Zone 1		2		3		4		5	
Year	Month		Surface	23m	Surface	23m	Surface	23m	Surface	23m	Surface	23m
							Temp. °C					
1945	July	...	...	...	...	...	...	...	...	...	...	...
	Aug.	...	19.0	9.0	...	...	21.5	15.8	...	...	...	...
1946	July	...	...	...	...	...	...	...	...	...	...	...
	Aug.	...	18.0	8.4	15.0	10.0	...	...	...	...	...	...
1947	July	...	21.0	15.5	20.5	9.4	20.2	6.6	19.3	...	20.8	...
	Aug.	...	18.4	15.6	...	...	...	...	...	...	...	...
1948	Aug.	...	...	...	...	...	19.6	9.4	20.2	6.6	...	...
1949	July	...	17.0	11.9	...	...	...	...	...	...	20.4	...
	Aug.	...	...	...	...	...	19.6	12.2	20.1	9.4	19.9	...
1950	July	...	18.8	10.4	...	...	18.5	14.4	18.5	...	...	...
	Aug.	...	18.7	12.0	...	...	18.5	10.0	...	...	19.2	9.8
1951	July	18.5(19.5)	17.2	5.6	...	...	...	...	18.0	4.2	...	...
	Aug.	18.7(19.2)	18.6	5.5	18.6	12.7	17.7	2.7	...	...	19.5	...
1952	July	19.8(20.1)	19.6	13.9	20.0	...	...	...	19.7	8.1	20.6	6.1
	Aug.	19.5(21.8)	18.8	...	...	...	...	...	21.2	6.0	20.6	4.4
1953	July	17.8(19.2)	17.2	7.2	...	...	...	...	...	...	...	...
	Aug.	18.7(20.0)	18.3	12.7	...	...	14.3	4.4	...	...	...	...
1954	July	... (19.3)	...	...	...	...	...	...	...	...	...	...
	Aug.	... (19.6)	...	...	...	...	...	...	...	...	...	...
1955	July	... (18.3)	...	...	...	...	...	...	...	...	19.4	...
	Aug.	18.9(19.9)	18.4	13.8	...	...	...	...	...	...	...	...
1956	July	... (18.6)	...	...	...	...	...	...	...	...	17.2	3.6
	Aug.	18.2(19.0)	19.0	...	...	...	17.3	15.6	18.4	8.4	...	...
1957	July	... (18.6)	...	...	...	...	...	...	...	...	...	...
	Aug.	... ...	...	...	...	...	...	...	...	...	...	...

SURFACE CONDITIONS

The irregularly recorded zonal surface temperature maxima usually varied between 18 and 20° and occasionally reached 21°C but were seldom recorded on the dates of peak monthly Borden temperatures. Furthermore, the observed al temperatures exceeded the corresponding Borden monthly maxima on a nber of occasions. In other words, conditions more extreme than those ibited in Table III probably occur frequently in the surface layer in all zones. en the thermocline teeters these surface conditions are likely to be established greater depths.

ALLOW WATER

Lauzier (1957) has shown that summer temperatures at depths of 20 m fath) normally fluctuate from 8 to 17°C. But he also shows that they may to 20° or higher when the thermocline is depressed and that they may fall 4° when the thermocline is elevated. These more extreme changes are more ly in the shallow parts of Zone 1 at the eastern end of Northumberland Strait, ere there are deep channels nearby, than at the western end where the bottom es more gently and where hydrographic conditions are generally more stable.

The rate of change with depth depends on the level of the thermocline.

ERMEDIATE DEPTHS

Temperatures at 23 m (13 fath) usually vary between 6 and 13°C but, as le III shows, they have been as low as 2.7°C (Zone 3, August 1951) when the rmocline was close to the surface and as high as 15.8° (Zone 3, August 1945) en the thermocline was deep.

A series of observations made on the same day as those reported in Table III Zone 1, July 1947, shows that there is much place-to-place variability in nmer temperature conditions. The tabulated records (21.0 and 15.5°C for ace and 23 m) apply to a station in the eastern part of the zone. Only a few es to the northwest and in the same zone the corresponding temperatures e 21.0 and 6.6°C. Further examples of local variation are given by Lauzier 57).

As already pointed out, Table III shows the highest zonal temperatures rded in an irregular series of observations. They were seldom taken on warmest days. It is safe to assume therefore that temperatures at 23 m en exceed those recorded and that under extreme conditions they may even roximate those at the surface.

The 23 m temperature is usually 10°C or higher in years when the thermocline eep and usually below 10° when the thermocline is close to the surface. Thus, en the thermocline is teetering and strongly depressed, the consequent perature changes at intermediate depths are likely to be greatest in those rs when the thermocline is closest to the surface.

EPER WATER

Summer conditions in deeper water (below 30 m or 17 fath) are not described Table III but Lauzier (1957) reports that summer temperatures fluctuate n 2 to 15°C as the thermocline teeters.

HYDROGRAPHY AND MASS MORTALITIES

Unaffected Gulf Beds

Deep southern Gulf beds are not affected. Toney River (Zone 2) is the most productive bed in Northumberland Strait and is deep, 31–37 m (17–20 fath). As shown above, summer temperatures on such deep beds are relatively stable and ordinarily range from 2 to 15°C. Only rarely could Toney River scallops be exposed to temperatures as high as 15°C and Fig. 2 shows that a shift from 2 to 15°C is well within their zone of thermal tolerance and therefore unlikely to produce lethal effects. This deep bed was discovered in 1955 and fished in 1956. It is significant that no mass mortality was detected on it in 1956 although there was a mortality that same year on the nearby Boughton Island Bed (Zone 1) which is at an intermediate depth (Table I). Similar statements can be made for other deep beds referred to in Table II.

Shallow beds in Zone 5 also seem little affected. They are well known from a long series of observations but only two slight mortalities have been reported (Table I). As shown above, temperatures are normally high and scallops accustomed to living under these conditions are not likely to be killed by the highest temperatures they are likely to experience when the thermocline is depressed (Table III and Fig. 2). Sudden temperature depressions may occur occasionally when the thermocline rises and these are not likely to be lethal.

Affected Beds

Mass mortalities are more frequent in the eastern part of Northumberland Strait (Zone 1) than elsewhere in the Gulf (Table I). The principal scallop bed in this zone, the Boughton Island Bed, has suffered at least six times since 1927. This and other affected beds of Zone 1 are at intermediate depths, 18–24 m (10–13 fath) on a sloping bottom. As seen above, scallops at this depth must be subject to frequent and often rigorous temperature changes caused by oscillations of the strongly developed thermocline. In this area there is good evidence that temperatures sometimes rise suddenly to lethal levels and produce mass mortalities (temperature kills) as Huntsman suspected.

Temperature kills. No on-the-spot temperature observations with a thermometer have ever been made in the Gulf just prior to, or during, a mass mortality. However, Mr Horace Hewitt of Montague, P.E.I., fished through the 20% Boughton Island (Zone 1) mortality of 1956 (Table I). And he gave an unsolicited report (personal communication) that when he caught the first dead scallops that year he was surprised to find them coming up from the bottom, warm to the touch. Normally they feel strikingly cold in summer, in contrast to the warm surface water. This is near proof that the thermocline had been suddenly depressed to the level of the scallop bed. Fig. 2 suggests that such a loss could have been brought about by a sudden rise in temperature from about 3 to about 20°C (Fig. 2). Our review of conditions at intermediate depths indicates that changes of approximately this order do occur there.

According to Mr Hewitt's account, dead animals appeared suddenly in his catches during both the 1946 and 1956 Boughton Island mortalities. Predators

no more abundant than usual and could scarcely have killed these scallops
uickly. They were probably killed by a temperature rise like that recorded
one 1, July 1947 but more extreme. The same explanation could apply to
even of the reported mortalities in this zone—40% in 1950, 30% in 1946,
in 1945, 90% in 1933 and 75% in 1928 (Table I). It could also apply to the
mortalities in Zone 2, "heavy" in 1928, 50% in 1949 and 40% in 1950; one
ne 3, 60% in 1928; one in Zone 4, 80% in 1933 and one in Zone 6, "heavy"
33.

The differences in percentage kills in these mortalities, despite similarities
her characteristics, may be attributed to differences in temperature acclima-
of the scallops involved; differences in the temperatures to which they were
enly exposed; and possibly also to differences in the lengths of time during
h they were exposed to the elevated temperatures.

The great extent of the scallop's zone of thermal tolerance probably explains
temperature kills are not more drastic and obvious. But they are un-
tedly more frequent than Table I suggests because our surveys of such a
area as the southern Gulf of St. Lawrence are necessarily sketchy. We
d never have been aware of many of the mortalities we studied if fishermen
not drawn our attention to them. And, from discussions with fishermen,
ave concluded that they report only the most spectacular of those they
ver. More than likely they fail to notice many minor mortalities.

Temperature debility and predator co-action. We have shown that
en raising or lowering of water temperature debilitates scallops and renders
temporarily incapable of reactions to avoid enemies. Debility of this sort
ost likely to occur in the Gulf of St. Lawrence than elsewhere because a
y mechanism for producing it seems to exist only there. And it may be
cted to occur there more widely and more frequently than temperature
first, because it requires temperature changes that are less extravagant
second, because it can be induced by either upward or downward temperature
ges. (Temperature kills follow only upward changes.) Presumably it
rred at intermediate depths in Zone 1 in July 1947 when conditions ap-
imated but did not attain the extremes required for a temperature kill
le III).

Chiasson (personal communication) has shown in tank experiments that
sh attack maimed scallops before they attack those that are whole. From
it can be anticipated that temperature debility would favour heavy preda-
It seems probable from Table I that both debility and predation (predators
abundant) were involved in the two Zone 5 mortalities (25% in 1929 and
in 1950) and in the single Zone 4 mortality (25% in 1929).

However, predation alone provides an explanation for some of these because
sson's tank experiment suggests that starfish concentrations such as were
on Richibucto Bed in 1950 may cause mortalities of the order observed
ut ancillary hydrographic causes. In support of this thesis it may be
er argued that conditions inducing debility of scallops may also debilitate
tors and therefore not appreciably affect the per cent mortality from

predation. This may have been true for the Richibucto Bed in 1950 because the lethal temperature for the common starfish is close to that for scallops.

Our view is that temperature debility could boost natural mortality of Gulf of St. Lawrence scallops by its co-active effects with predation. But it is impossible to determine its contribution to total natural mortality by field observations alone. From what we have seen it may be assumed that at maximum the co-actionary effects of debility and predation approach 25% as they appear to have done on Richibucto Bed (Zone 5) in 1950.

CONCLUSIONS

There have been many mass mortalities of scallops in the Gulf of St. Lawrence but it is apparent that all do not have the same explanation. Starvation, senescence, disease and weakness at spawning time seem very unlikely causes. Disease, predators, temperature debility and the direct lethal effects of exposure to lethally high water temperatures have been considered as likely causes.

Scallop stocks outside the Gulf of St. Lawrence and those on the deepest beds in the Gulf show annual natural mortality rates approximating 10%. Hydrographic conditions are relatively stable in these areas and the scallop stocks are free of mass mortalities.

The peculiar hydrographic phenomena of the upper layers of the southern Gulf of St. Lawrence waters permit great and sudden increases and decreases in water temperature on beds at intermediate and shallow depths. The assembled records provide good evidence that these are great enough to cause mass debility of scallop populations. And temperature debility seems to co-act with predation to produce the higher than normal natural mortalities (up to about 25%) and was probably involved in several of the Gulf mortalities.

However, predation, either alone or co-acting with temperature debility, is likely to be a slow process and could scarcely account for the sudden and most drastic losses (up to 80%) such as the wide-spread mortality in 1933, the heavy mortalities in Zone 2 (Pictou Island) in 1949 and 1950 and the frequent mortalities on beds at intermediate depths in Zone 1. These have been encountered nowhere else on this coast and from our knowledge of the temperature tolerance of scallops and of the unique hydrographic conditions which obtain in the vicinity of Gulf scallop beds, we conclude that these mortalities were high-temperature kills. Apparently these result from teeterings of the thermocline which flood the beds with warm water of the surface layer.

ACKNOWLEDGMENTS

We wish to acknowledge our debt to Drs L. P. Chiasson, A. G. Huntsman and A. W. H. Needler. We have drawn freely from their written and oral accounts of mortalities and their speculations about causes. We are especially grateful to Dr L. M. Lauzier for his assistance with the parts of this paper which deal with hydrography.

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Lethal Temperatures of the Developmental Stages of the Sea Lamprey, *Petromyzon marinus* L.[1,2]

By R. W. McCauley[3]

Fisheries Research Board of Canada
Biological Station, London, Ont.

ABSTRACT

Of all stages of the sea lamprey, the eggs have the most exacting thermal requirements. range of constant temperatures necessary for successful hatching is narrow, being 15–25°C. range may be extended to 12–26°C and possibly beyond, if the eggs have developed to the stage before they encounter temperature extremes.

The ability to withstand high temperature characteristic of the post-embryonic stages of the ies appears shortly before or after hatching.

The role of temperature in the development of eggs under natural conditions is discussed.

INTRODUCTION

IS a general observation that the thermal requirements of the embryonic ges of fish are more demanding than those of the post-embryonic stages. rphogenesis is brought about by many interdependent chemical and physical cesses, and since these have different temperature coefficients, temperature nges may disturb the harmony necessary for normal development. Post-ryonic forms are able to adjust to changes by "physiological compensation" y, 1958). Some of these mechanisms which allow the organism to adjust temperature changes probably require functioning organ systems. This pensation is obviously lacking in the early embryonic forms.

In the present study attention was focussed on the temperature range over ch eggs of *Petromyzon marinus* L. can develop in relation to the upper lethal perature of its post-hatching stages.

The natural history of the landlocked sea lamprey, *Petromyzon marinus* L., been studied in detail by a number of workers, e.g., Applegate (1950), gley (1956). Eggs are laid in late spring on the redds and within two weeks ch into prolarvae. In the following three weeks the prolarvae continue elopment, absorb their yolks and become larvae. As larvae they spend eral years in the sediments of streams feeding upon microorganisms in the er. The duration of larval life, estimated to lie between four and seven rs, is terminated by metamorphosis during the last year of larval life.

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[1] Received for publication September 5, 1962.

[2] This project was supported under contract by the Great Lakes Fishery Commission. It also ed part of a thesis submitted for partial fulfilment of the requirements for the degree of Doctor hilosophy in the Department of Zoology at the University of Western Ontario.

[3] Present address: Ontario Department of Lands and Forests, Fish and Wildlife Division, hern Research Station, Maple, Ontario.

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ted in Canada.

Metamorphosis involves a change in behaviour, in that a secretive animal becomes an active predator. The career of a predaceous lamprey in the lake varies from one to one and a half years before the lamprey returns to the stream and spawns. In the present investigation, the life history of a lamprey has been divided into an egg stage lasting days, a prolarval stage lasting weeks, a larval stage lasting years, a predaceous stage lasting one to one and a half years, and a spawning stage lasting months.

MATERIALS AND METHODS

Lethal temperatures of the developmental stages were determined by three methods. Data were available from Piavis (1961) who found that sea lamprey eggs could develop to the hatching stage at constant temperatures spanning the range 15–21°C. These experiments were repeated in part not only to confirm or delimit further this temperature range, but also to provide prolarvae of known thermal history for lethal temperature tests. The technique of rearing eggs was similar to that of Piavis. Eggs were artificially fertilized at 18°C and placed in Petri dishes resting on the bottom of 20-litre aquaria filled with creek water maintained at a constant temperature. Circulation around the eggs was provided by a single air stone inserted several centimeters over the center of the bottom of the aquarium. Batches of eggs were reared at constant temperatures of 15, 18, 20 and 25°C, and the percentage hatch at each of these temperatures recorded.

In the second method, subsamples of the prolarvae which had hatched at the constant temperatures mentioned above, were transferred directly into a series of constant temperature baths maintained at lethal or near lethal temperatures. The time to attain 50% mortality in each subsample was calculated. Since the pattern of mortality of the animals in the lethal test baths was similar to that observed in adult fish undergoing thermal death, the data were treated by the statistics customarily used to express the lethal temperatures of fish (Brett, 1952). Straight lines relating lethal temperatures to the logarithm of the median time to death were plotted and these taken as expressions of the thermal resistance. The data in this form could then be compared with similar lines obtained from the post-embryonic forms in a previous study (McCauley, 1962).

In the third method the limitations of experiments at constant temperatures were recognized. During the spawning season temperature is not constant but fluctuates. A complete analysis of the effects of fluctuating temperatures would be complicated. Such variables as the rate of change of temperature, the time during development at which the change occurs, and the effects of previous thermal experience of the embryo would have to be taken into consideration. A demonstration, however, was given of the effects of drastic temperature changes during development by initially fertilizing and rearing a sample of eggs at 18°C and transferring subsamples directly at consecutive days of development to other constant temperatures above and below this value. The new series of rearing temperatures were 12, 14, 23 and 26°C respectively. The embryos were allowed to continue their development at these new temperatures and the number of prolarvae which hatched was recorded.

RESULTS

VELOPMENT AT CONSTANT TEMPERATURES

A varying proportion of the eggs reared at the four constant temperatures eloped to the prolarval stage (Table 1). Prolarvae of the 25°C sample were racteristically deformed being usually bent at right angles -a deformity ed by Piavis in lamprey embryos incubated at high temperatures. The tionship between percentage hatch and rearing temperature is suggested in 1 by a curve drawn with due regard to the paucity of points especially for peratures in the vicinity of 18°C. Since the percentage hatches summarized Table 1 refer to four separate experiments their comparison is questionable.

TABLE I. Percentage hatch of samples of sea lamprey eggs reared at various constant temperatures.

	Eggs fertilized	Rearing temperature (°C)	Time to hatch (days)	No. of eggs	Percentage hatch
I	June 29, 1960	15	11	750	23
		20	6	6400	28
		25	6	250	11
II	July 8, 1960	15	11	2000	3.5
		20	...	...	...
		25	6	1000	5
III	July 26, 1961	18	6	1400	54

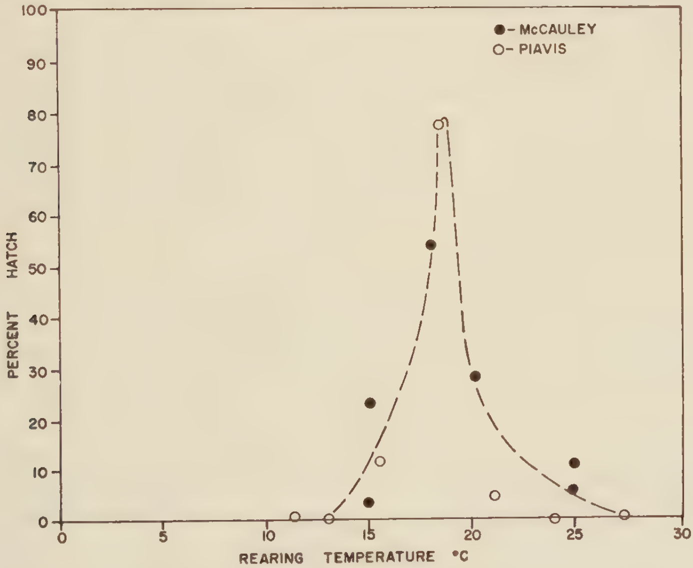

FIG. 1. Relationship between rearing temperature and percentage hatch in samples of sea lamprey eggs.

Consequently the relationship depicted is provisional, pending additional data. Whatever the exact shape of the curve may be, it is evident that the range of constant temperatures over which sea lamprey eggs can hatch is approximately ten Centigrade degrees.

Attempts to obtain additional data from other batches of fertilized eggs were unsuccessful. The reproductive period of the sea lamprey is about one month and it was hoped to extend this period artificially, so that brood stock would be available over a longer period. Spawning-phase individuals were collected early in the spring and their sexual maturity retarded by holding them in the laboratory at 5°C. At convenient intervals throughout the summer they were brought into maturity by either transferring them to other constant-temperature tanks maintained at 20°C or to cages immersed in Big and Medway Creeks (Norfolk and Middlesex Counties, respectively). By these two techniques, sexually mature lampreys were available as late as September of the same year. However, the fertilized eggs provided by these specimens did not develop beyond early cleavage, after which time they disintegrated. No reason for this lack of viability was evident, but when the necessity of using individuals which had matured during the spawning season was recognized, the season had passed.

Experiments in which Temperature is Changed During Development

Post-hatching stages

The prolarvae reared at 25°C were malformed and died erratically at the high lethal test temperatures. The data of these moribund animals were not used in the description of the resistance of prolarvae to high temperature. The data of the groups reared at 15 and 20°C were combined because of their close similarity and a straight line drawn through the points. The line relating test temperature to the logarithm of the median time to death is shown in Fig. 2. Such lines are usually terminated on the right at a temperature which is no longer lethal after an exposure of infinitely long duration. In practice, the duration of this time is about a week. It was, however, impractical to subject the prolarvae to longer periods, since at this stage transformation to larvae occurs within two weeks.

Pre-hatching stages

The control sample reared at 18°C produced a percentage hatch of 54%. The percentage hatches of subsamples removed from the control sample at different times of development are summarized in Table II. In general the later the transfer was made during the period of development, the greater was the percentage hatch. There is some evidence that the sudden transfer from the control temperature to the test temperature may have caused thermal shock. Although 23°C falls within the range of constant temperatures over which lamprey eggs can develop to hatching, the subsample transferred to this temperature at the 64-cell stage did not develop. Thus lethal effects in the subsamples at the test temperatures may have been caused not only by the sojourn at the temperature but also by the temperature shock experienced in transfer.

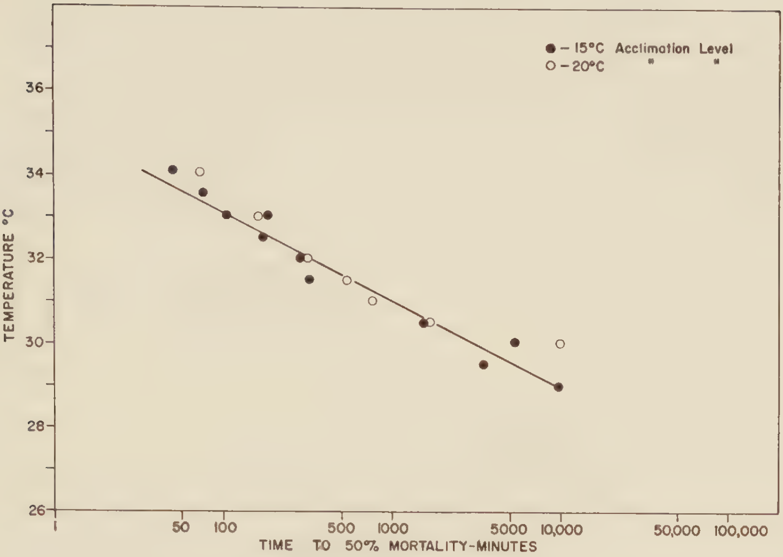

FIG. 2. Upper lethal temperatures of prolarvae hatched at 15 and 20°C.

TABLE II. Percentage hatch in subsamples of 200 eggs reared initially at 18°C and transferred to higher and lower temperatures at various stages of development (hatched embryos counted 15 days after fertilization).

Transfer made at		Percentage hatch at final rearing temperatures (°C)[a]			
Time	Stage	12	14	23	26
1 day	64 cells	0	0	0	0
2 days	full blastula	0	0	3	0
3 days	gastrula	0	0	8	0
4 days	neural plate	0	1	12	0
6 days	head	5	2	14	5
8 days	prehatching	29	7	25	23

[a] 54% hatch in eggs left at 18°C.

Prolarvae which hatched at all temperatures except 12°C were indistinguishable in appearance from those of the control group. Those hatched at this temperature were smaller.

DISCUSSION

The relatively narrow limits of temperature required by lamprey embryos for normal development are in keeping with the general principle that the thermal requirements of the embryonic stages of fish are demanding. The lethal temperatures of pre- and post-hatching forms are difficult to compare since the mechanisms of thermal death are likely different in both groups. In Fig. 3 the thermal requirements of lamprey eggs for development are compared graphically with the upper lethal temperatures of the post-hatching stages. All the upper lethal temperatures determined for the post-hatching stages (prolarvae, larvae, parasitic and spawning phase adults) for acclimation levels between 2 and 30°C are included in the area shaded with oblique lines. The details of acclimation and the techniques of determining the upper lethal temperatures of the post-hatching forms are contained in a thesis (McCauley, 1962).

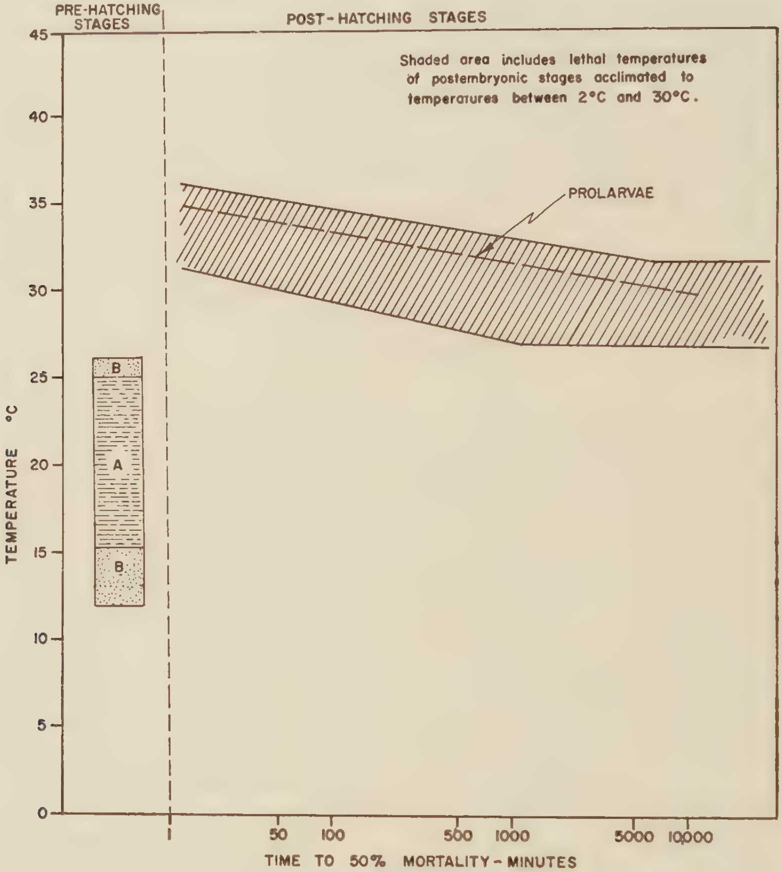

FIG. 3. Lethal temperatures of pre- and post-hatching stages of *P. marinus*. The upper lethal temperatures of the post-embryonic forms are taken from McCauley (1962). **A**. Range of constant temperatures over which some eggs of a sample can hatch (from Table I). **B**. Range of temperature which can be withstood by late pre-hatching stages (from Table II).

Experiments in which temperature is changed during development suggest that the range for development is somewhat wider. Thus some proportion of a sample of lamprey eggs can hatch at temperatures between 12 and 26°C and possibly beyond these limits, provided temperature extremes are encountered late in development. The results of the present experiments are in agreement with those of other authors who either fertilized and reared lamprey eggs artificially (Whitfield, 1948; Lawrie and Lamsa, 1954 (personal communication); Lennon, 1955; Wigley, 1956), or recorded temperatures during development of lamprey eggs in the stream (Coventry, 1922; Applegate, 1950; Skidmore, 1958).

Piavis' (1961) original study established the range of constant temperatures over which some proportion of a sample of lamprey eggs can hatch. He had reservations in applying his results to stream conditions, since fluctuating rather than constant temperatures are the rule. Some field observations of stream temperature during the development of lamprey eggs include temperatures outside this range (Coventry, 1922; Applegate, 1950; Skidmore, 1958). The laboratory experiments in which temperature is changed show that temperatures in the range of 12 to 26°C could be tolerated in streams during development. In general, the embryos can withstand temperature extremes if they occur late in development. A relationship between the thermal regime of a stream during the spawning period and the number of young-of-the-year larvae produced would be difficult, if not impossible, to establish. Each of the many lots of fertilized eggs deposited on the redds experiences its own particular thermal regime. Only in exceptional situations, where temperatures persist at lethally high or low levels throughout development throughout the season, would all embryos fail to develop.

Lethal temperatures of fish quoted in the literature have usually been determined on individuals of the post-embryonic stages (Brett, 1956). Bishai (1960) investigated the upper lethal temperatures of larval salmonids at various acclimation temperatures. Pearson's data (1951) for the upper lethal temperature of brown trout (*Salmo fario*) may be compared with Bishai's results for alevins of the same species. At the lowest acclimation level (5°C) the upper lethal temperature of both groups was 22.5°C. At an acclimation level of 20°C, however, the upper lethal temperature of the fingerlings was almost two degrees higher than the alevins. Since Bishai had to limit the period of thermal acclimation of the larvae to a period of less than seven days, a period probably inadequate, the fish may not have been fully acclimated. The comparisons afforded by lethal temperatures of larval and post-embryonic forms of *Salmo fario* and *Petromyzon marinus* suggest that fish develop those mechanisms that permit them to resist high temperature soon before or after hatching. Additional data for other species are required to test this hypothesis.

ACKNOWLEGMENTS

Mr J. A. Sholdice, Student Assistant, gave valuable help in the rearing of the specimens and in conducting lethal temperature experiments.

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Intraseasonal Growth in Lake Superior Lake Trout[1]

By A. H. Lawrie

Fisheries Research Board of Canada
Biological Station, London, Ont.

ABSTRACT

Intraseasonal growth curves for lake trout, *Cristivomer namaycush* (Walbaum), of Lake Superior are deduced from a consideration of the increment in the number of circuli outside the last annulus of the scales as the season (1961) progressed. These curves are generally sigmoid and differ from one another in ways which suggest that they define differences in the onset, rate and duration of growth in the groups of fish concerned. However, the relationship between this measure of scale growth and the more conventional dimensional measures of both scale and fish growth have not been established.

INTRODUCTION

Descriptions of growth rates have been presented for many populations of lake trout, *Cristivomer namaycush* (Walbaum), throughout its range. Martin (1951), Webster *et al.* (1959) and Rawson (1961) provide convenient references to the papers concerned. In general, these accounts have been concerned with the rate of increase in size, usually length, from year to year. The nature of growth within a season has rarely been defined.

From returns of tagged trout, Fry (1953) showed that the intraseasonal growth of South Bay, Lake Huron trout fitted a sigmoid curve at least to the point of inflection. Kennedy (1954) also deduced an intraseasonal growth curve of this form for Great Slave Lake trout of commercial size from a consideration of the progressive increase in the antero-lateral radius of the scales through the growing season. In the present account, it is shown that the increase, through the growing season, in the number of circuli outside the last annulus of the scales of Lake Superior trout of commercial size is also sigmoid in character.

MATERIALS AND METHODS

Scales were obtained during the course of routine, net-run sampling of entire commercial catches in the various statistical districts of Lake Superior (Fig. 1) in 1961. The great majority of the catches were made in large-mesh nylon gill nets ($4\frac{1}{2}$–5 inch (11–13 cm) stretched measure), but limited samples were obtained from smaller mesh sizes ($2\frac{1}{2}$–3 inch (6–8 cm) stretched measure) and from pound nets, especially in western districts.

So far as possible, scales were consistently taken from the left side of the fish midway between the lateral line and the dorsal fin. Readings were made from the magnified image of the water-mounted scale projected in the conven-

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[1] Received for publication September 18, 1962.

J. Fish. Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

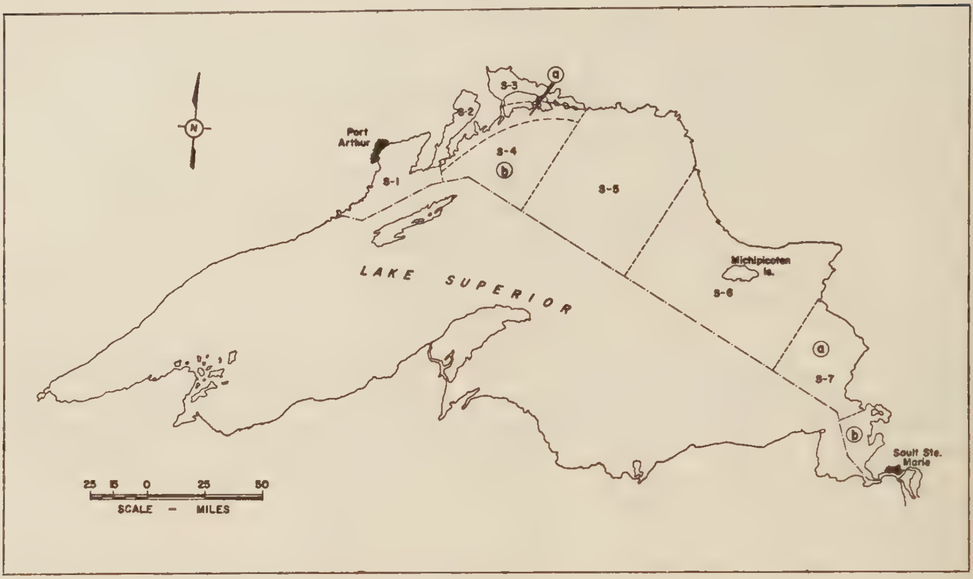

FIG. 1. The fishery statistical districts of Lake Superior.

tional manner. The number of circuli outside the last annulus, including that normally considered to bound the annulus, was counted in the posterior field and routinely recorded along with the age (the number of completed annuli) for each scale. Each reading, both of the number of annuli and of the number of circuli, was determined by the examination of several scales from each fish. All circuli, including those interrupted by breaks in other parts of the scale, were counted. Consistency tests indicated approximately 90 and 70% agreement in repeated readings of age and circuli count respectively. In cases of disagreement, the variation in circuli count was of the order of plus or minus two.

For the past several years, very substantial numbers of hatchery-reared lake trout have been planted into the lake, usually as yearlings, by the United States Fish and Wildlife Service and the Conservation Departments of the States of Michigan and Wisconsin in United States waters, and by the Ontario Department of Lands and Forests in Canadian waters. To facilitate subsequent recognition, these fish were all marked prior to planting by the removal of certain fins in such a way that, given the age of a planted fish, identification as to origin is certain. Owing to their limited numbers, planted lake trout have been omitted from this analysis which deals exclusively with native fish.

RESULTS

The mean number of circuli outside the last annulus was calculated for each age represented in the collections from each month in each statistical district for which a reasonable number of scales were available throughout the season. These data are presented for Statistical Districts S-1, S-4a and S-7a in Table I.

TABLE I. Mean number of circuli outside the last annulus of the scales of native lake trout from Statistical Districts S-1, S-4a and S-7a, Lake Superior, 1961. (Sample sizes in parentheses.)

	Mean number of circuli at age								
Month	II	III	IV	V	VI	VII	VIII	IX	X
				Statistical District S-1					
Feb.	...	...	...	0.0 (1)	0.0 (1)	...	...	...	...
Mar.	...	...	...	...	...	...	...	...	...
Apr.	...	...	...	0.0 (2)	0.0 (1)	...	...	...	...
May	...	1.6 (5)	1.0 (25)	1.1 (158)	0.9 (117)	0.4 (65)	0.4 (13)	...	...
June	...	...	1.0 (1)	1.0 (9)	1.3 (7)	0.5 (2)	...	...	...
July	...	4.0 (1)	3.2 (5)	3.6 (5)	3.0 (5)	...	2.7 (3)	1.5 (4)	...
Aug.	...	4.1 (8)	3.6 (7)	3.5 (13)	3.4 (9)	5.5 (2)	...	1.0 (1)	...
Sept.	...	6.2 (20)	6.2 (40)	6.1 (48)	6.0 (108)	5.7 (64)	5.3 (8)	5.0 (1)	...
Oct.	...	8.0 (2)	8.8 (13)	8.6 (136)	8.1 (399)	7.4 (98)	7.4 (12)	7.3 (3)	...
Nov.	...	9.8 (8)	8.2 (6)	7.8 (21)	8.1 (56)	7.1 (23)	...	6.0 (1)	...
				Statistical District S-4a					
Feb.	...	...	...	0.0 (7)	0.0 (3)	...	...	...	...
Mar.	...	0.0 (1)	0.0 (3)	0.0 (9)	0.0 (26)	0.0 (6)	...	...	...
Apr.	...	0.0 (5)	0.1 (50)	0.1 (119)	0.0 (124)	0.0 (52)	0.0 (4)	0.0 (1)	...
May	...	1.0 (1)	1.0 (53)	0.7 (128)	0.4 (225)	0.3 (121)	0.1 (8)	0.0 (1)	0.0(1)
June	...	1.4 (8)	1.6 (33)	1.7 (76)	1.5 (145)	0.8 (68)	0.0 (2)	0.0 (1)	...
July	5.0 (2)	5.1 (10)	4.1 (39)	4.0 (86)	4.2 (106)	3.6 (66)	3.0 (1)	6.0 (1)	...
Aug.	6.0 (1)	6.6 (3)	6.6 (8)	6.1 (8)	5.7 (20)	5.8 (12)	4.0 (1)	...	...
Sept.	...	8.0 (1)	6.3 (8)	6.6 (92)	6.6 (157)	6.6 (36)	5.7 (3)	...	...
Oct.	...	7.0 (1)	7.5 (13)	7.6 (69)	7.7 (84)	7.3 (20)	...	...	...
				Statistical District S-7a					
Feb.	...	...	...	...	...	...	...	...	...
Mar.	...	...	...	0.1 (9)	0.1 (12)	...	...	...	...
Apr.	...	0.6 (33)	0.8 (32)	0.7 (74)	0.6 (97)	1.0 (4)	1.0 (1)	...	...
May	...	0.5 (6)	1.1 (15)	0.9 (52)	0.8 (145)	0.4 (103)	0.3 (17)	0.0 (3)	...
June	...	4.0 (1)	...	1.9 (15)	2.2 (50)	2.0 (53)	1.1 (18)	0.5 (4)	...
July	...	3.0 (1)	4.0 (9)	4.6 (30)	3.9 (68)	3.5 (80)	3.9 (8)	...	...
Aug.	6.5 (2)	7.0 (7)	6.8 (23)	6.5 (21)	6.7 (95)	6.3 (31)	5.0 (1)	...	...
Sept.	...	...	6.5 (2)	6.6 (7)	6.7 (59)	5.6 (21)	5.3 (3)	...	...
Oct.	7.0 (2)	...	6.4 (7)	7.2 (11)	6.8 (42)	6.3 (48)	6.4 (7)	...	...
Nov.	...	7.8 (5)	7.5 (17)	7.7 (11)	7.2 (32)	7.5 (13)	...	...	...

Among other things, inspection of the data in Table I suggests a correlation between age and the rate at which new circuli are laid down, older fish being slower growing. A rigorous demonstration of the extent of the correlation has not been attempted. However, an apparent effect of month to month changes in age distribution is illustrated by Fig. 2 which shows for Statistical Districts S-4a and S-7a the decline, through the early part of the growing season, in the number of trout showing no new growth. Table II shows that in District S-4a the age distributions remained essentially constant from month to month, whereas in contrast monthly mean ages of District S-7a samples varied widely

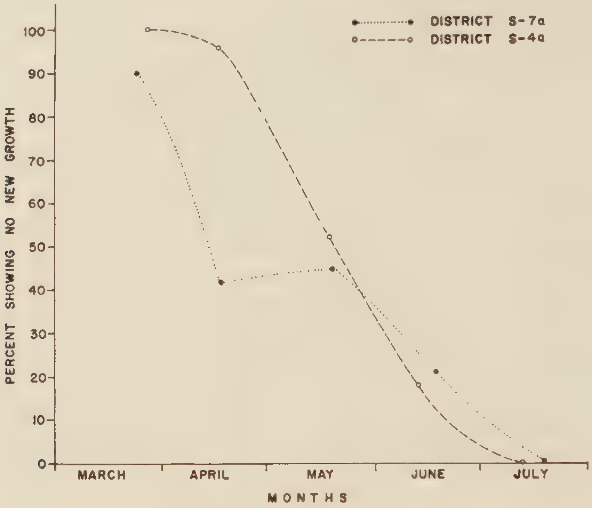

FIG. 2. The percentage of lake trout from Districts S-4a and S-7a, Lake Superior, whose scales show no sign of new growth (zero circuli outside the last annulus) during the spring of 1961. Monthly values plotted at the mean date of each monthly sampling period.

TABLE II. Mean ages of lake trout sampled each month in Statistical Districts S-4a and S-7a, Lake Superior. (Number of samples in parentheses.)

	Mean ages			
Month	Statistical District S-4a		Statistical District S-7a	
Feb.	5.3	(10)	...	...
Mar.	5.7	(45)	5.6	(21)
Apr.	5.5	(355)	5.0	(241)
May	5.8	(538)	6.1	(341)
June	5.7	(333)	6.6	(141)
July	5.6	(311)	6.2	(196)
Aug.	5.6	(53)	5.7	(180)
Sept.	5.8	(297)	6.2	(92)
Oct.	5.6	(187)	6.2	(117)
Nov.	...	...	5.4	(78)

and erratically. There can be little doubt that these changes in the age distributions of the monthly samples account for the abrupt inflections in the curve for District S-7a.

The form of the intraseasonal growth curves, fitted by eye, for the three districts of Table I is presented for Age VI fish (the best represented age) in Fig. 3. Similar curves can be drawn for other ages and appear to form, along with those shown, a family of curves for each district of essentially the same shape. Since the curves for each district are different, not only in the time of origin and the asymptotic value reached but also in shape, they would appear

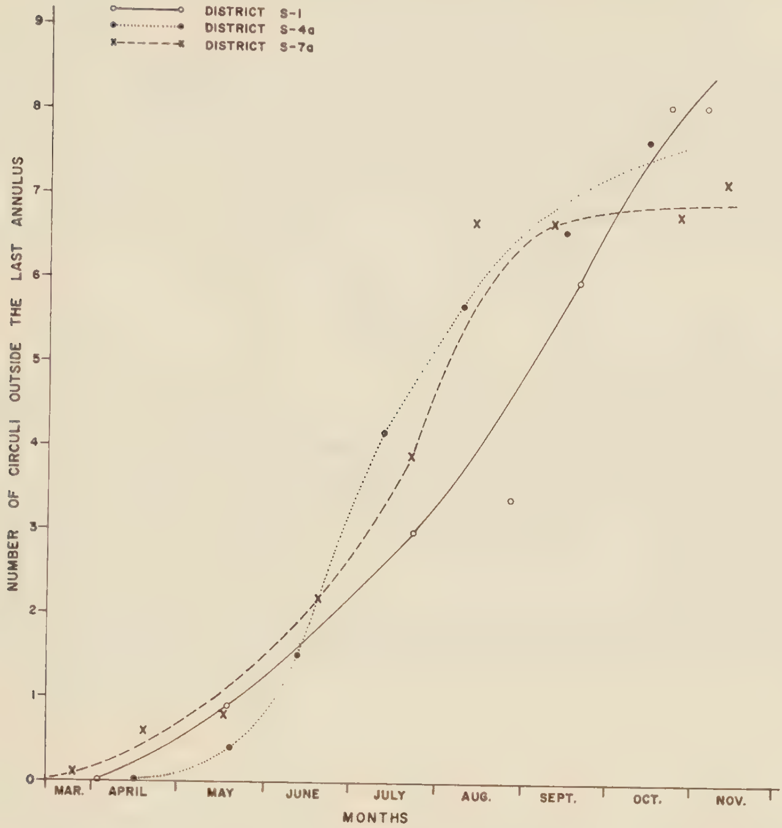

FIG. 3. Intraseasonal growth in the scales of Age VI lake trout from Statistical Districts S-1, S-4a and S-7a, Lake Superior, during 1961. Monthly values plotted at the mean date of each monthly sampling period.

to define real differences in the growth of the scales if not the fish from the respective districts.

The fact that the curve for District S-7a is virtually asymptotic by late October or early November, while those for the other two districts are approaching this condition at that time, suggests that there may be virtually no winter growth. Supporting this view is the fact that the few mid-winter scales available show no signs of continued growth and are scarcely distinguishable from late fall scales. Essentially, the same condition was noted by Kennedy (1954) for Great Slave Lake trout.

DISCUSSION

Although circuli counts can be readily made and appear to provide a convenient means of defining intraseasonal growth and hence the prospect of assessing differences between groups of fish, it should be noted that the relationship of this numerical description of scale growth to the more usual dimensional treatment has not been established. Still less is its relationship to the growth of the fish known.

ACKNOWLEDGMENTS

Various members of the staff of the Station, especially Messrs R. M. Hanson, C. C. Parker and A. G. Ryder, have been responsible for collection of the scales in the field, and Mrs Irene Weir has been both faithful and painstaking in reading them. Messrs R. M. Hanson and D. V. Browne assisted materially in the analysis. This technical assistance is gratefully acknowledged.

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Discards of Fish at Sea by Northern New Brunswick Draggers[1]

By Yves Jean

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

Sampling aboard northern New Brunswick draggers from 1956 to 1961 shows a substantial reduction in the percentage by numbers and by weight of the catch of cod discarded at sea. The total numbers of cod discarded in the southwestern Gulf of St. Lawrence, which amounted to about 7 million in 1956, have been reduced to an estimated 1 million in 1961. Two factors are mainly responsible for this reduction: large-mesh nets which, following an ICNAF recommendation, became effective in 1957, and reduction in sizes retained for landing. The mesh effect is believed to be 1.3 times greater than the cull effect in reducing cod discards in 1961. Discards of American plaice have increased during the same period, due to larger recruitment of young year classes. Discards of species other than cod and plaice are negligible because they are only a small part of the catch. Survival experiments show that most cod and plaice are dead when returned to the sea. The use of large-mesh codends may result in long-term increase in the total cod landings in the southwestern Gulf of St. Lawrence.

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INTRODUCTION

The management of groundfish fisheries in the northwest Atlantic is based on continuous investigations of the effects of fishing on stocks, catch and landings. Evaluation of the quantities, sizes and ages of fish landed is now a routine assessment for many stocks. However, the additional fishing mortality attributed to the capture of unmarketable fish which are discarded at sea has not been studied in many fisheries. This paper describes the results of a six-year study of wastage of groundfish at sea from draggers fishing off northern New Brunswick, Canada, in the southwestern Gulf of St. Lawrence (Fig. 1). Discards are found to represent a significant portion of the catch of cod and

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[1] Received for publication March 26, 1962.

J. Fish. Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

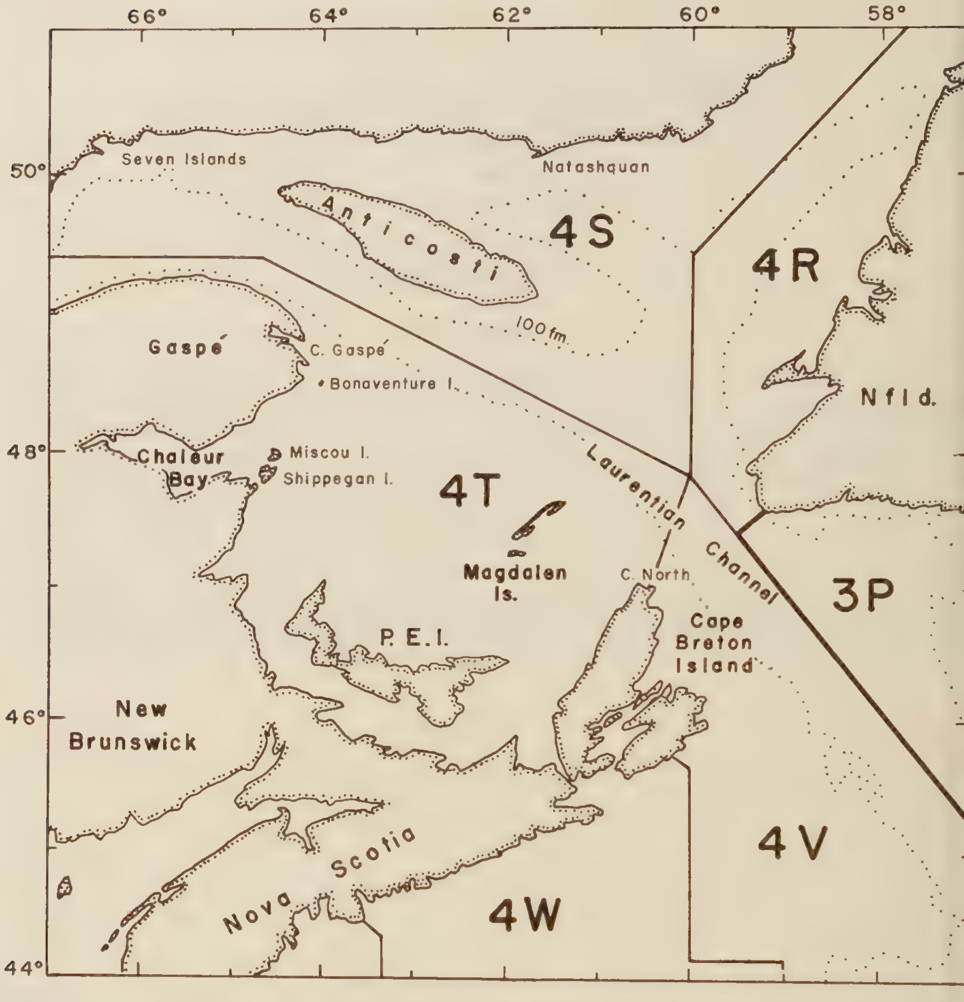
66°
64°
62°
60°
58°
50°
48°
46°
44°
Seven Islands
Natashquan
Anticosti
4S
4R
100 fm
Gaspé
C. Gaspé
Bonaventure I.
Nfld.
Chaleur Bay
Miscou I.
Shippegan I.
4T
Laurentian Channel
Magdalen Is.
C. North
3P
P. E. I.
Cape Breton Island
New Brunswick
Nova Scotia
4V
4W

FIG. 1. Map of the Gulf of St. Lawrence showing localities mentioned in the text and ICNAF Division boundaries. The southern boundary of 4V (39°00′ N Lat.) is not shown.

plaice. Survival studies show that a large proportion of these discarded fish die without contributing to current or future landings. The effects of gear selection, quantities and sizes of fish caught and market acceptability are examined. The results are pertinent to consideration of conservation and utilization of the groundfish resources of the Gulf of St. Lawrence.

Prior to the end of World War II the groundfish fishery of the southwester Gulf of St. Lawrence was carried out almost entirely with baited hooks and lines and jiggers. Shortly after the war a major change took place with the introduction of otter trawls. The first small otter trawlers, commonly called draggers, began operation in 1947 in northern New Brunswick and in 1951 in Quebec. The otter-trawl fleet expanded rapidly, and in 1960 more than 13

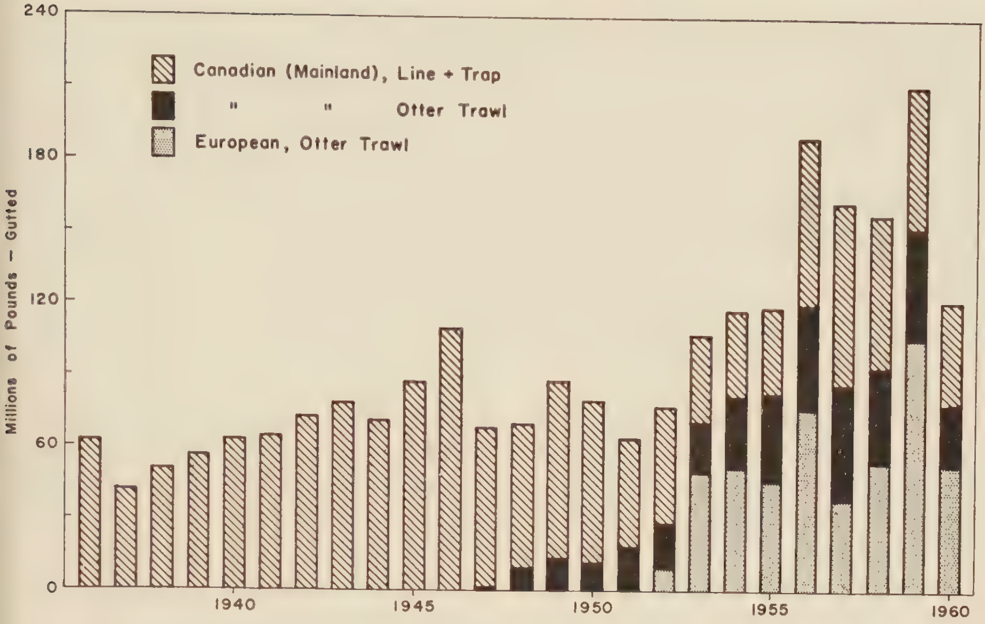

FIG. 2. Annual cod landings from the southwestern Gulf of St. Lawrence (ICNAF Divisions 4T and 4V (spring only)) by countries and by gears, 1936 to 1960. (From: Canada, Fisheries Statistics and ICNAF Statistical Bulletins).

draggers from Quebec and the Maritime Provinces were fishing in the southwestern Gulf of St. Lawrence.

Following the introduction of the otter trawl, and probably as a result of it, the annual cod landings by all countries fishing in the southwestern Gulf of St. Lawrence (ICNAF Divisions 4T and 4V (spring), Fig. 1) more than doubled. Annual landings averaged 61 million lb[2] during the decade 1937-49 immediately preceding the introduction of draggers, compared with 133 million lb during the 1951-60 period (Fig. 2). Prior to 1947 nearly all cod landings from the southwestern Gulf of St. Lawrence came from lines, whereas in 1960 more than 60% were caught by otter trawl, both Canadian and European (Fig. 2). About one-third of the Canadian landings by all gears from the southwestern Gulf is now landed by northern New Brunswick draggers (Canada, Fisheries Statistics).

The otter trawl as a fishing gear is efficient, but it can be wasteful, especially if used with small-mesh codends. Large quantities of fish too small to be of any commercial value are brought on deck and are later discarded. It is also wasteful in time, since the discarding of small fish and other trash slows down fishing operations.

As a conservation measure the International Commission for the Northwest Atlantic Fisheries (ICNAF) at its 1955 Annual Meeting (Bates 1955) recommended that the member countries fishing for cod and haddock in Subarea 4 (Canadian Atlantic coast) use a minimum mesh size of 4½ inches (114 mm) for manila, or its equivalent for other fibres, to replace the 3-inch (76 mm) o smaller mesh used during the early years of otter trawling in Subarea 4. Inside knots measurements were to be taken with a wedge-shaped, flat gauge inserte in the lumen of the mesh with a pressure of 10 to 15 lb (4.5 to 6.8 kg) while th net is still wet after use. Following the ICNAF recommendation, Canad passed a regulation which made the $4\frac{1}{2}$-inch mesh mandatory in February 1957 The recommendation was also accepted by other countries and by the end o 1958, the $4\frac{1}{2}$-inch mesh regulation was in effect for all countries fishing i Subarea 4. In northern New Brunswick, the years 1957 and 1958 were year of transition when part of the fleet adopted the new regulation mesh and par retained the pre-regulation one. In 1959 the conversion to the $4\frac{1}{2}$-inch mes was complete.

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[2] Unless otherwise indicated, weights are in pounds, gutted, head-on. Conversion factors to round fresh weight = 1.2; to metric tons: 1 metric ton = 2204.6 lb.

Factors other than mesh size may determine the portion of the catc rejected at sea. The size composition of the catch, distribution of small fis and market requirements are some of them. These factors are subject to annua and long-term variations. The purpose of the present paper is to evaluate th effects of the various factors on the discards of small fish in the Gulf of St Lawrence in recent years.

MATERIALS AND METHODS

SAMPLING AT SEA

From 1956 to 1961 our observers measured discards on 44 trips aboar commercial draggers of various sizes. The length, gross tonnage, trawl specifications and total numbers of sampling trips for each class of draggers are given i Table I.

TABLE I. Number of sampling trips made from 1956 to 1961 aboard various classes of dragger fishing in the southwestern Gulf of St. Lawrence.

Type of boat	No. of sampling trips	Length in feet	Gross tonnage	Otter trawl		
				No.	Headrope in feet	Footrope in feet
Chaleur	5	46	26	35	35	52
Gloucester	17	54 – 57	35 – 48	35	50	70
"Name boats"	21	60 – 67	55 – 62	35	50	70
	1			36	60	80

The Chaleur draggers operate mainly in Chaleur Bay and in the shallo waters off Miscou and Shippegan Islands (Fig. 1). The Gloucester and 60-foo (18.3 m) draggers fish the deeper waters off Bonaventure Island and along th western slope of the Laurentian Channel from Cape North to Cape Gaspé, a well as the shoaler waters around Miscou, Shippegan and the Magdalen Island In 1960 and 1961, due to the scarcity of fish in the southwestern Gulf, the Quebe and New Brunswick draggers made several trips to the north shore of the Gu and fished the coastal waters from Seven Islands to Natashquan.

Methods of Estimating Discards

The percentage of fish discarded at sea may be calculated by one of four principal methods (Keir, 1959, 1960):

1. Measuring a sample of the catch (before discards) at sea and comparing this with a sample of the landings at the wharf. The number of fish above the 100% retention length (i.e. the size at which all fish are kept for landing) are equalized in sea and wharf samples. The difference in numbers in adjusted sea and shore samples represents the numbers discarded from the sample of the catch. These are expressed in per cent of the catch. From a length–weight curve numbers discarded are converted into weights which are also expressed in per cent of the catch.

2. Measuring all discards at sea, or a sample supplemented by a count of the discards not measured, and a wharf sample of the landings. From the average weight per fish landed the total weight landed is converted into total numbers. These, plus total numbers discarded, represent total numbers caught. Percentage discards by numbers and by weight are calculated as above.

3. Measuring a sample of the catch at sea before discards and measuring all discards or a sample as in 2. In this case a length–weight relationship is used to determine the weight of the sample of the catch. From the total weight landed the sample is raised to total weight caught, i.e. weight discarded plus weight landed, and to total numbers caught. Percentage discards, by numbers and by weight, are calculated as in 1 and 2.

4. Recording estimates of weights caught and discarded after each tow in the log book. Total estimated weight caught less weight discarded during a trip should approximate the actual weight landed. Percentage discards by weight are calculated directly from the estimated catch.

The first method was the one generally used throughout this study. In 1960 and 1961 the relatively small numbers of cod discarded at sea made it possible on some trips to measure all cod discarded as well as a sample of the catch and of the landings. This provided an opportunity to compare the various methods of estimating discards.

During the period 1956–61 discards were calculated mostly for cod (*Gadus morhua* Linnaeus) and to a lesser extent for American plaice (*Hippoglossoides platessoides* (Fabricius)). The number of cod measured at sea varied from 1500 to 3500 and those measured at the wharf varied from 300 to 700 per trip. Samples of about 400 plaice from both catch and landings of some trips were measured. All cod were measured from the tip of the snout to the fork of the caudal fin (fork length). Plaice were measured from the tip of the snout to the tip of the rounded tail (total length). All measurements were taken to the nearest centimetre.

COD DISCARDS

Cod and plaice are the dominant species in the landings of commercial draggers fishing in the southwestern Gulf of St. Lawrence (Table II). In 1960 cod made up 57% and plaice 31% of landings by Gloucester-type draggers.

TABLE II. Total landings by 35 Gloucester-type draggers fishing in the southwestern Gulf o St. Lawrence in 1960.

Species	Landings[a]	
	'000 lb	%
Cod (*Gadus morhua* (Linnaeus))	9,129	57
American plaice (*Hippoglossoides platessoides* (Fabricius))	4,919	31
Winter flounder (*Pseudopleuronectes americanus* (Walbaum))	473	3
Witch flounder (*Glyptocephalus cynoglossus* (Linnaeus))	440	3
Haddock (*Melanogrammus aeglefinus* (Linnaeus))	396	2
Hake (*Urophycis* spp.)	336	2
Redfish (*Sebastes marinus* (Linnaeus))	166	1
Miscellaneous	36	<1
Total:	15,895	

[a] Cod, haddock and hake gutted, head-on; others round.

TABLE III. Average cod discards as percentage of total catch during sampling trips aboard commercial draggers from 1956 to 1961. Minimum and maximum percentages are shown in parentheses.

Year	Trips	Cod discards	
		By number	By weight
	no.	%	%
1956	7	25 (15 – 59)	9 (1 – 29)
1957	10	24 (3 – 65)	6 (1 – 21)
1958	10	16 (10 – 33)	7 (3 – 14)
1959	9	13 (1 – 22)	6 (<1 – 11)
1960	5	10 (6 – 15)	4 (2 – 6)
1961	3[a]	6 (<1 – 16)	2 (<1 – 7)

[a] Data based on 3 sampling trips and log records of 43 commercial trips; see text.

Percentage discards of cod for all sampling trips in each of the years 1956 to 1961 are given by count and by weight in Table III. These are the differences between total catch and total landings of all sampling trips made during one year, expressed as percentage of the catch.

FACTORS AFFECTING DISCARDS

Table III shows a wide range in percentage discards each year and a gradual decrease from 1956 to 1961. Large variations in the portion of the catch discarded at sea have been observed from trip to trip throughout this study. Before discussing the decrease in cod wastage in the Gulf of St. Lawrence in recent years, let us examine the various factors affecting the proportion of the catch discarded at sea by commercial draggers.

MESH SIZE. The size of the mesh used, especially in the codend, obviously affects discards: the larger the mesh the smaller the number of undersized cod retained and the lower the percentage discarded. This was shown by Martin and Jean (1958) who compared data collected in 1957 during three sampling trips with small-mesh codends (about 3-inch) with data from three trips with large-mesh (about 4½-inch) manila codends. They found that discards of cod with small-mesh codends were 31% by number and 10% by weight, compared to 12% and 5%, respectively, with large-mesh codends.

The year 1958, the second year of conversion to large-mesh nets, provided another opportunity to compare discards from small- and large-mesh nets. From May 26 to August 16, nine comparable trips were made on the Bonaventure Island grounds (Fig. 1), four on draggers using small-mesh (3-inch) and five on draggers using large-mesh (4½-inch) manila codends. The size composition of cod caught with small-mesh and large-mesh codends is compared in Fig. 3. Cod discards with small-mesh codends were 23% by number and 9% by weight compared with 12% by number and 5% by weight with larger-mesh codends. The 1958 observations confirm those of Martin and Jean (1958) in showing that discards with small-mesh codends were about double those with large-mesh codends on the same fishing grounds.

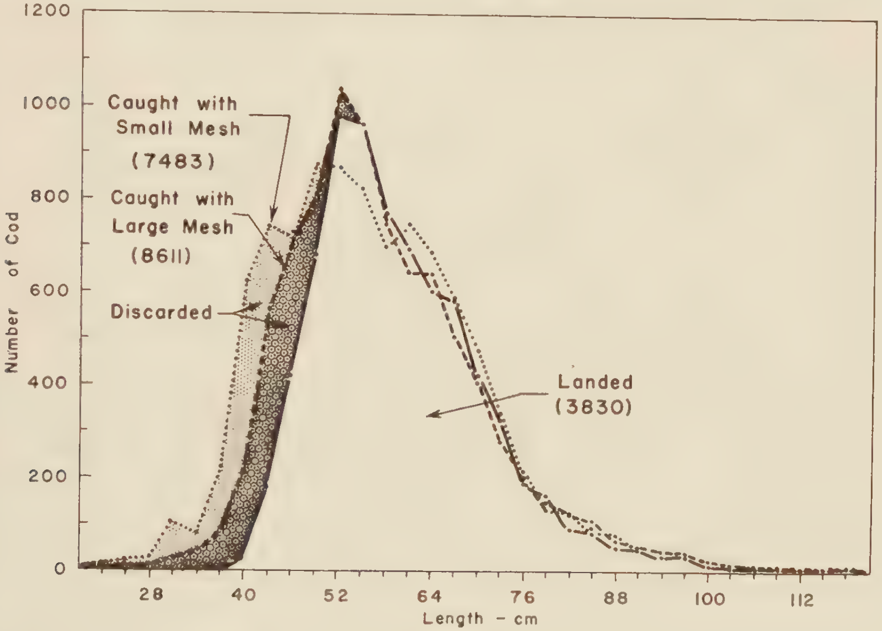

FIG. 3. Size compositions of cod caught with small-mesh (3-inch) and large-mesh (4½-inch) codends and of cod landed from sampling trips aboard northern New Brunswick draggers in 1958. Numbers of fish in the samples are in parentheses.

ABUNDANCE OF SCROD. The percentage discarded is also affected by the relative abundance of scrod (cod below 51 cm in length, and 2 lb or 0.9 kg in weight). This is shown in Fig. 4 where percentage discards by numbers are plotted against the ratio of numbers of scrod to total cod in the catch. To eliminate the effects of area fished and mesh size on discards, only trips made in

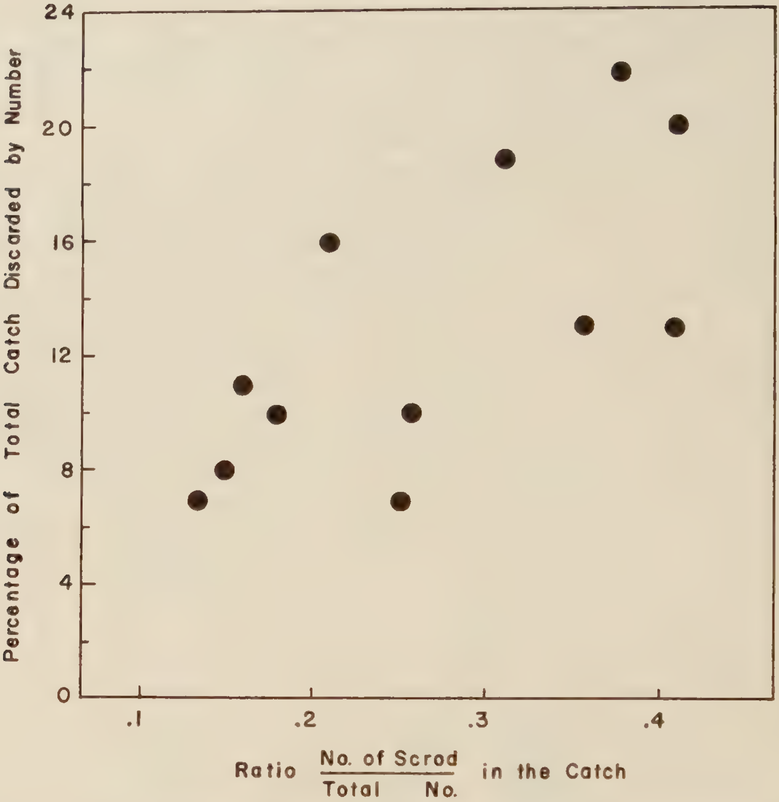

FIG. 4. Relationship between the proportion of scrod (below 51 cm) in the catch and the percentage discarded. Each point represents one trip.

the Bonaventure Island area aboard draggers with large-mesh (4½-inch) codends were considered. Twelve trips made during the years 1957 to 1959 were selected on that basis. Large-mesh nets were not introduced until 1957 and no manila codends were used on the sampling trips made in 1960 and 1961. As seen in Fig. 4, larger percentages were discarded when small fish formed a higher proportion of the total catch. Presumably the larger the proportion of scrod in the catch, the greater is the incentive for the crew to discard low-priced, fast-spoiling, small cod.

CONCENTRATIONS OF SMALL COD. The percentage of the catch discarded at sea also varies with local concentrations of small cod. Trips made on grounds where small cod are relatively more abundant generally show larger percentages of discards. Recent cod taggings in the Gulf of St. Lawrence in summer (McCracken, 1959, 1961) and off the east coast of Cape Breton in winter (Martin, 1961) have shown that cod migrate into deep water and out of the Gulf in late fall and return to the Gulf in late spring. Annual groundfish surveys carried out in the Gulf of St. Lawrence and east of Cape Breton since 1957 (Jean, 1960) indicate that small cod (40 cm and smaller) are concentrated in shoal waters in the spring and to a still greater extent in the fall. In winter these small cod migrate into deeper water but not as far south along the Laurentian Channel as the larger ones. The seasonal concentration of small fish in shoal waters of the Gulf is likely due to the fact that the small cod are the first ones to move inshore in the spring and the last ones to leave in the fall. These small fish are found in spring and autumn at depths of 20 fathoms (37 m) or less southeast of Shippegan and Miscou Flats (Fig. 1) and in Chaleur Bay (Marcotte, 1959). Draggers fishing on these grounds catch and discard large numbers of small cod. This is shown in Table IV where discards on the Chaleur Bay and Shippegan Island grounds are compared with those off Bonaventure Island during the years for which comparable data are available. Percentage discards were from 2 to 3 times higher in the Chaleur Bay–Shippegan Island area.

TABLE IV. Comparison of per cent discards of cod in (A) the Chaleur Bay and Shippegan Island area, and (B) in the Bonaventure Island area, during the years 1956 and 1958.

			Discards			
			By number		By weight	
Year	Average mesh size	Trips	A	B	A	B
	inches	*no.*	%	%	%	%
1956	3	7	55	18	14	4
1958	4½	6	26	12	10	5

SIZES RETAINED FOR LANDING. The wastage data collected in 1959 provided an opportunity to observe how sizes selected for landing (cull at sea) may affect the percentage of cod discarded. Cull at sea in turn is affected by such factors as grading at the plant, as was the case in 1959. This was the first year when all northern New Brunswick draggers used large-mesh (about 4½-inch) codends. Consequently all sampling trips were made on draggers with large-mesh nets and were comparable. This was also a year when the sampling trips covered the longest period, from early June to early September. The percentages by number discarded on 9 sampling trips in 1959 are shown in Fig. 5B. From the first part of the summer until about July 24 discards were low, averaging about 3%. Toward the end of July discards increased sharply and averaged about 20% until September. The size composition of cod caught during these two periods did not differ markedly, and was not responsible for the sudden increase in discards. The 50% retention length for landing, i.e. the length at which half the fish caught are retained and half are discarded, on the other hand, increased from 41 cm prior to July 24 to 45 cm after that date. The change in cull at sea, which resulted in higher discards, followed a change in grading at the Caraquet shore plant (Fig. 5A). Early in the season less than 10% of the cod landed by Caraquet draggers were graded as low-priced scrod. This percentage rose to

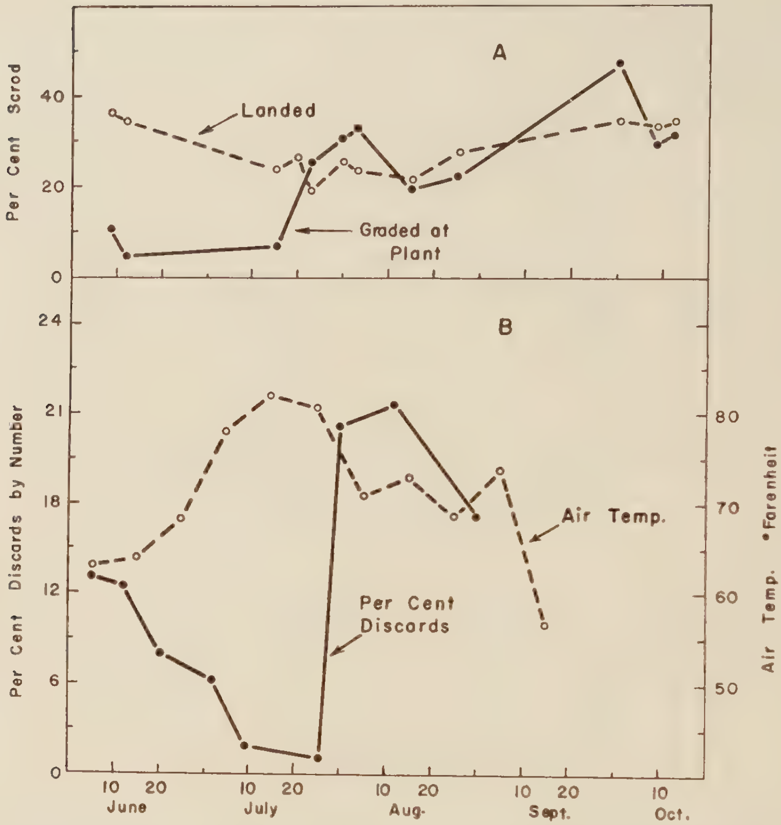

FIG. 5. A: Percentage of scrod cod landed by northern New Brunswick draggers and percentage graded as scrod at a local plant at Caraquet, N.B., in 1959. B. Per cent discards of cod aboard commercial draggers and maximum air temperatures in 10-day averages at Miscou Island in 1959. (Temperatures from Canada, Department of Transport).

about 30% during the latter part of July. The change in grading at the plant coincided with the peak in summer air temperatures (Fig. 5B) which caused small fish to spoil more rapidly. As a result of stricter grading at the plant, fishermen changed their cull at sea. Discards of small, fast-spoiling fish increased accordingly. Wastage remained high until September, the end of the observation period in 1959.

The above analysis shows that size of mesh, relative abundance of scrod in the catch, local concentrations of small cod and sizes retained for landing are important factors affecting percentage of discards. Other factors, such as distances from fishing grounds to landing port and individual differences in grading by the crew at sea, were mentioned in observers' reports as influencing discards. The data, however, are insufficient to show the effects of these factors.

COMPARISON OF RESULTS BY VARIOUS METHODS OF ESTIMATING DISCARDS

Actual numbers of cod discarded at sea in 1960 and 1961 were rather small. This provided an opportunity to measure all discards in addition to samples of the catch and of the landings on two trips in 1960 and two trips in 1961 (Table V). From these data a comparison of the four methods of calculating discards (described on page 501) was made. The results are summarized in Table VI. For the sake of clarity, only discards by weight are given.

TABLE V. Summary of cod sampling aboard New Brunswick draggers in 1960-61 on trips where catch, discards and landings were measured.

Year	Trips	Tows	Tows sampled for catch	Cod measured before discards	Discards measured	Cod measured at wharf
	no.	*no.*	*no.*	*no.*	*no.*	*no.*
1960	2	30	12	1,620	1,422	563
	4	26	13	1,605	1,568	727
1961	1	23	13	1,470	250	423
	2	37	14	1,807	197	395

TABLE VI. Percentage discards, by weight, of cod taken during four sampling trips made in 1960 and 1961. Discards were calculated using four methods as follows: 1 = catch and landings; 2 = discards and landings; 3 = catch and discards; 4 = observer's log-book estimate; see text, page 501.

Year	Trips	Total weight landed	Total weight discarded	Discards by weight using methods 1	2	3	4
	no.	*lb*	*lb*	%	%	%	%
1960	2	25,455	1,394	6	5	4	3
	4	21,615	1,882	8	8	7	6
1961	1	18,130	243	1	1	2	2
	2	34,340	154	1	1	1	1

Method 2, based on actual numbers discarded and actual total landings, is the most direct (Keir, 1959) and probably the most reliable. However, Table VI shows that the results obtained by the other methods do not differ appreciably from those obtained by Method 2. Although all four methods of calculating discards are subject to errors in sampling (Methods 1 to 3) or in estimating weights of catch and discards (Method 4), the results are in fairly close agreement.

Based on the 1960 results, a variant of Method 2 (discards and landings) was introduced in 1961. A number of dragger captains were asked to record on special forms the actual numbers of cod discarded at sea after each tow. The total landings were obtained from purchase slips at the end of the trip.

A small fee was given to the crew member who counted the discards. In addition, sampling of discards (brought ashore by commercial draggers or measured at sea by our observer) and of landings was carried out at regular intervals. The size compositions of discards and landings provided the necessary data to convert numbers discarded into weight, and weight landed into numbers.

Dragger captains contacted before 50 trips brought in reliable discard records from 47 trips. Data from 43 of these log records were used and included in Table III in calculating the 1961 discards. The remaining four were not used because of a lack of data on the size composition of discards in the Chaleur Bay area where the trips were made.

Table VI shows that comparable discard figures are derived from sampling any combination of catch, discards or landings. They also show that the actual count of discards by fishermen, plus occasional sampling of discards and landings, allow a greater coverage of the fishing fleet. Log-book estimates of discards by weight, supplemented by actual sampling of catch, discards and landings, would also provide an adequate coverage of the fleet.

Size Composition of Cod Discards

A knowledge of the size and age compositions of the catch is essential for the assessment of fish stocks. Such parameters as fishing mortality, recruitment and age at first capture are estimated from catch data. Most sampling, however, is done on landings. If sizes and quantities discarded are known, sizes and quantities caught can be derived from those of the landings.

Data on the size composition of discards in the southwestern Gulf of St. Lawrence were collected on two trips in 1960 and three trips in 1961. On two of the 1961 trips samples of discards were brought ashore by the dragger captains and measured at the wharf by our observer. Total cod discards were measured at sea by observers during all other trips. The percentage size composition of discards is given in Table VII.

The size composition of cod discarded at sea during these two years did not vary markedly. Few fish below 28 cm were caught and discarded. Almost all cod caught above 46 cm were retained. In both years the mean length of discards was about 39 cm. The mean weight, estimated from a length–weight relationship, was 1 lb (0.5 kg).

DISCARDS OF SPECIES OTHER THAN COD

Although cod is the main commercial species caught and landed by northern New Brunswick draggers, other species represent an appreciable portion of the total landings (Table II).

Plaice

American plaice, which accounted for 31% of the total 1960 landings, is the second most important species landed by draggers fishing in the southwestern Gulf of St. Lawrence. This species also occupied second rank in the catches of research-vessel hauls (ca. 3-inch mesh codend) in the Miscou–Bonaventure Island area in 1953 (Jean, 1954).

TABLE VII. Percentage size composition of cod discarded at sea by northern New Brunswick draggers using 4½-inch mesh codends in 1960 and 1961.

Length groups	Frequency 1960	1961
cm	%	%
22	0.3	...
25	0.7	...
28	3.5	0.3
31	6.2	4.0
34	9.1	11.6
37	18.6	15.6
40	30.5	34.7
43	24.1	29.5
46	6.5	4.0
49	0.5	...
No. of fish	1,525	351
Mean length, *cm*	38.9	39.5
Mean weight, *lb*	1.0	1.0

TABLE VIII. Observers' log-book estimates of American plaice discarded by northern New Brunswick draggers, 1956 to 1961.

Year	Sampling trips	Estimated catch	Actual landings	Discards by weight
	no.	*lb*	*lb*	%
1956	4	32,339	26,718	17
1957	8	19,096	16,603	13
1958	10	48,421	39,850	18
1959	9	37,044	29,520	20
1960	3	8,960	5,816	34
1961	2	5,076	2,500	51

On most sampling trips the weight of plaice caught and of plaice discarded, as estimated in consultation with the skipper, was entered in the observer's log book after each haul. An estimate of total discards by weight was obtained for each trip. From the actual weight landed and the log-book estimate of discards, the total weight caught was calculated. Total catch and total landings from the sampling trips of one year were added. From these data annual percentage discards by weight were calculated (Table VIII).

The sea- and wharf-sampling method used throughout this investigation in estimating cod discards is sometimes inapplicable to the American plaice. This was the case in 1960 when large plaice, well above the 100% retention length, were discarded because of the "jellied" condition of their flesh (Templeman and Andrews, 1956; Powles, 1961). In this case, it was impossible to equalize sea and shore samples in order to calculate numbers and weight of small fish discarded. The jellied condition was not observed during the plaice-sampling trips made in 1958 and 1959. It is reasonable to assume that no large plaice were discarded during these trips. The sea- and shore-sampling method indicates that plaice discards by weight in the southwestern Gulf of St. Lawrence amounted to 34% in 1958 and 64% in 1959. By applying theoretical selection curves to survey data, Powles (1960) estimated that plaice discards by numbers were 70% in 1957, 74% in 1958 and 81% in 1959. These would correspond to percentage weights of about 40% in 1957 and 60% in 1959. On the basis of research-vessel catch, Jean (1954) estimated that 87% by count of plaice caught in 1953 on the Bonaventure and Miscou Islands grounds were discarded. The corresponding figure by weight is estimated at about 60%.

The above percentages by weight of plaice discarded are considerably higher than the observer's log-book estimates given in Table VIII. This may be due to the fact that it is rather difficult to estimate the quantities of plaice in the codend or in deck checkers partly filled with cod and other species. The observer's log-book data probably underestimated the quantities of plaice discarded at sea. Figures in Table VIII, however, indicate that, in contrast to cod (Table III), plaice discards increased from 1956 to 1961, despite larger mesh sizes. Based on data from surveys with fine-mesh codends, Powles (1960) attributed the increase in wastage of plaice to an increase in the relative numbers of plaice below 35 cm in the catch.

INCIDENTAL MARKETABLE SPECIES

Incidental species of commercial interest, i.e. species other than cod and plaice, which in 1960 made up about 12% of the total landings (Table II), were discarded to a varying extent. This is shown in Table IX, based on our observer's log-book entries for 1959, the year with the largest number of sea trips aboard large-mesh draggers.

Commercial log records indicate that northern New Brunswick draggers fish about 1600 hours (800 hauls) during a normal fishing season. From the data shown in Table IX, the total discards per boat per fishing season in 1959 were about 400 lb of winter flounder and 380 lb of haddock. Discards of hake (*Urophycis* spp.) were around 6000 lb. All witch flounder (*Glyptocephalus cynoglossus* (Linnaeus)) caught were of marketable size and none were discarded. It is estimated that about 10% by weight of the incidental commercial species caught are discarded.

INCIDENTAL UNMARKETABLE SPECIES

Other species of no commercial value are discarded. These include: skates (*Raja* spp.), eelpouts (*Macrozoarces americanus* (Bloch and Schneider) and *Lycodes* spp.), lumpfish (*Cyclopterus lumpus* (Linnaeus)), sea ravens (*Hemitripterus americanus* (Gmelin)), sculpins (*Myoxocephalus* spp.) and spiny dogfish (*Squalus acanthias* (Linnaeus)). Except for skates, which have an average frequency of

TABLE IX. Log-book estimates of discards of marketable species other than cod and plaice caught during 9 sea trips in the southwestern Gulf of St. Lawrence in 1959.

Species	Average catch per hour[a]	Discards by weight
	lb	%
Winter flounder	5	5
Witch flounder	17	0
Haddock	12	2
Hake	4	95
Redfish	1	100[b]

[a]From commercial log records.
[b]Discarded on cod trips.

occurrence of about 3 per haul, the above non-commercial species occur at the rate of 5 to 8 fish per 10 hauls. On the basis of 800 hauls per fishing season, the average number of individual fish of non-commercial species discarded at sea in 1959 was about 3000 fish per boat. At 2 lb per fish, as roughly estimated by our observer, the total weight of non-commercial species discarded was about 6000 lb per boat per fishing season.

The occasional halibut (*Hippoglossus hippoglossus* (Linnaeus)), turbot (*Reinhardtius hippoglossoides* (Walbaum)) and shad (*Alosa sapidissima* (Wilson)) are kept and consumed by the crew.

In summary, observations collected at sea aboard northern New Brunswick draggers show that cod discards have decreased from 9% to 2% by weight during the period 1956–61. Plaice discards, based on log-book estimates, have increased from about 13% to 50% during the same period. It is estimated that about 10% by weight of the catch of incidental species of commercial value caught are discarded. The other unmarketable fish species caught are discarded.

SURVIVAL OF DISCARDED COD AND PLAICE

Undersized cod and plaice remain on the deck of commercial draggers from 15 to 30 minutes before being shovelled overboard. According to our observers' reports, most of the discarded fish are dead by the time they are discarded. To obtain information on the survival of cod and plaice left on deck, survival tests were carried out during night fishing from the research vessel *A. T. Cameron* in October 1960. Four series of tests, two on cod and two on plaice, were made on four different nights. Cod were divided into 4 lots and plaice into 3 lots, according to size. Different lots were left on deck in a uniform manner, i.e. in a single layer, for periods of time varying from less than 5 minutes to 45 minutes. After exposure, the fish were placed in tanks filled with sea water. The numbers of fish alive were noted after they had been in the tank for 1 hour (except for one series with plaice when they were kept in tanks from 1 to 2 hours). Temperatures at the sea bottom, as well as air and tank temperatures, were recorded.

Cod

The results of two series of experiments conducted on cod on October 6 and 8, 1960, are summarized in Table X. Cod less than 40 cm long had a lower survival rate than the larger ones. In the first series of tests none of the small cod survived a 30-minute exposure on deck, whereas up to 13% of the larger ones survived. In the second series of tests, 20% of the small ones compared to 80% of the larger ones survived.

Table X. Survival of cod after exposure on deck of the *A. T. Cameron* for varying periods of time in October 1960; for air temperature, high = 4.4° to 7.8°C and low = − 1.1° to 0.6°C.

Exposure, *minutes:*	<5	5		15		30		45
	Series	Series		Series		Series		Series
	1	1	2	1	2	1	2	2
Air temperature	High	High	Low	High	Low	High	Low	Low
Tank temp., °*C*	11.4	11.5	6.6	11.6	6.7	11.6	6.5	6.4
Bottom temp., °*C*	1.9	3.8	3.6	10.6	2.0	4.4	1.1	1.0
Size groups *cm*				Survival, %				
20 – 29	20	10	70	20	60	0	20	0
30 – 39	50	60	78	40	40	0	20	0
40 – 49	50	70	90	70	90	10	50	10
50 – 59	100	67	87	50	90	13	80	20
All sizes	51	50	81	45	70	6	43	8

Air temperature (and possibly water temperature in the tanks) affected survival of cod after exposure on deck. The first series of tests was carried out at air temperatures varying from 4.4° to 7.8°C (the mean water temperature in the tanks being about 11.5°C). The second series of experiments was conducted at air temperatures of 0.6° to − 1.1°C (tank temperature of about 6.5°C). As seen in Table X, the survival of cod exposed to warmer air temperatures was consistently lower than that of cod of the same size exposed to colder air temperatures. The same results were obtained when all sizes were lumped together (Fig. 6). These observations show that a greater percentage of cod survive a given length of exposure on deck when the air temperature (and possibly the tank temperature) is lower.

Plaice

Experiments on survival of plaice after exposure on deck were carried out on October 4 and 5, 1960. The results are summarized in Table XI. As in the case of cod, the smaller plaice (less than 30 cm) generally had a lower survival rate than the larger ones. Less than 10% of the small plaice survived a 30-minute exposure, compared to 20% of the larger ones. Differences in air temperatures during the two series of tests on plaice survival were not as large as in the case of cod. This may account for the fact that no consistent differences in survival rates of plaice were observed between the two series of tests (Table XI).

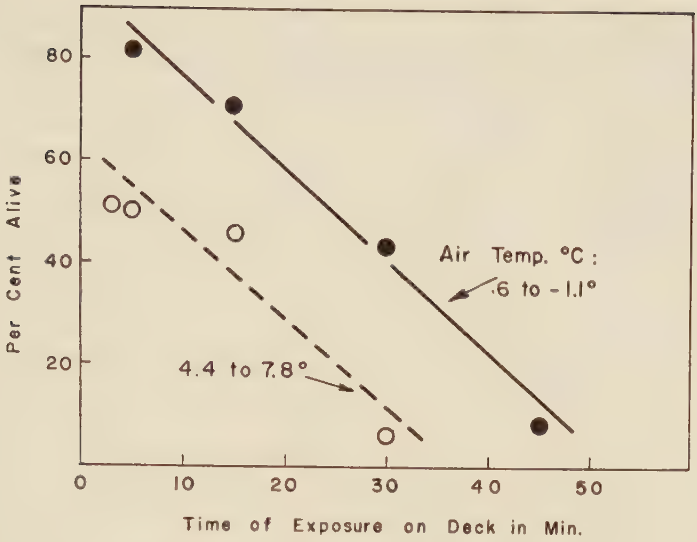

FIG. 6. Effects of time of exposure on deck and air temperature on survival of cod 20 to 59 cm long.

Cod and plaice appear to be equally vulnerable to exposure on deck. One series of tests on cod and two on plaice were carried out at roughly comparable air temperatures, i.e. from 2.2° to 7.8°C (Tables X and XI). Survival of cod and plaice of all sizes after varying exposures on deck are compared in Fig. 7. No consistent differences in the percentages of fish which survived exposure were observed between the two species.

These experiments show that the chances of survival of small cod and plaice discarded at sea from commercial draggers are rather poor. All cod below 40 cm (Table X) and most of the plaice below 30 cm (Table XI) died after a 30-minute

TABLE XI. Survival of plaice after exposure on deck of the *A. T. Cameron* for varying periods of time in October 1960.

Exposure, *minutes*:	<10		15		30		45	
	Series		Series		Series		Series	
	1	2	1	2	1	2	1	2
Air temperature, °*C*	4.4	7.2	4.4	4.4	2.8	4.4	2.2	5.0
Tank temp., °*C*[a]	10.6	10.0	10.0	10.2	9.7	10.1	10.0	9.7
Bottom temp., °*C*	1.5	0.7	1.8	0.6	1.6	0.7	1.6	0.7
Size groups *cm*	Survival, %							
10 – 19	40	27	13	0	0	0	0	0
20 – 29	78	100	40	20	0	10	30	0
30 – 39	78	92	78	40	20	20	0	0
All sizes	64	74	44	27	7	10	17	0

[a] Fish kept in tank from 1 to 2 hours in Series 1, and for 1 hour in Series 2.

exposure on deck when the air temperature was below 8°C. It is unlikely that small cod and plaice would survive even shorter exposures when summer air temperatures reach an average of 22°C (Fig. 5B). It is concluded that the majority of cod and plaice discarded at sea by northern New Brunswick draggers are dead when thrown overboard.

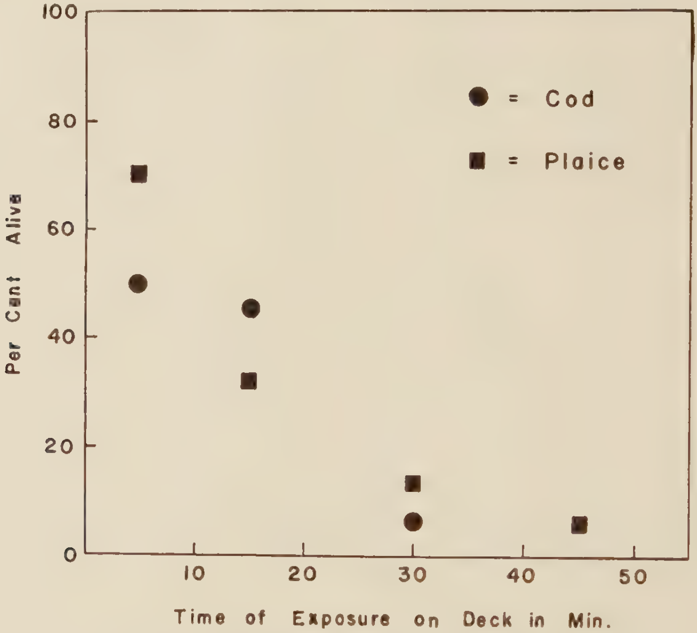

FIG. 7. Survival of cod and plaice after exposure on deck for varying periods of time.

DISCUSSION

Selection studies summarized by Clark *et al.* (1958) show that the selective properties vary quite widely with different gear and, within one gear, with mesh or hook size. McCracken (1957), using Marcotte's (1952) data, showed that the 50% selection length of No. 14 hooks, generally used by line fishermen in the Gulf of St. Lawrence, was about 48 cm, corresponding to a weight of about 1¾ lb (0.8 kg). Small-mesh (3-inch) manila codends in use in the Gulf fishery for about 10 years prior to mesh regulation have a 50% retention length of less than 30 cm (about ½ lb or 0.2 kg). Larger-mesh manila codends (4½-inch) introduced in 1957 have a 50% retention length of 40 cm (1¼ lb). Synthetic codends of the same mesh size have a slightly higher selection, 43 cm, corresponding to a weight of about 1½ lb (0.7 kg).

On theoretical grounds one would expect that the introduction of otter trawling in the southwestern Gulf of St. Lawrence in 1947 resulted in smaller fish being caught and landed. That this was so is indicated by the decline in salt-fish production, which depends on large fish. During the decade 1930-39 about

90% of the total southwestern Gulf cod landings were salted (Canada, Fisheries Statistics). During the decade 1950–59 this figure has decreased to 62%. In the year 1959 alone, salt-fish production amounted to only 39% of the total landings.

The gradual shift toward smaller fish in the catch and landings of cod has continued even after the introduction of large-mesh nets in the Gulf, as shown in Fig. 8. The percentage size compositions of cod caught and landed by draggers using large-mesh codends during the years 1957 to 1961 are compared. An increase in percentage of scrod and a decrease in percentage of large cod in both catch and landings are evident from Fig. 8. Smaller fish are now caught and retained for landing. This is further evident when selection curves for landing are compared for the years 1957 to 1961 (Fig. 9). The 50% retention length for landing with large mesh has decreased from about 45 cm in 1957 to 40 cm in 1961.

The preceding section has shown that mesh size, relative abundance of scrod in the catch, area fished and sizes selected for landing (cull) are important factors affecting discards. From the above discussion it is evident than an increase in

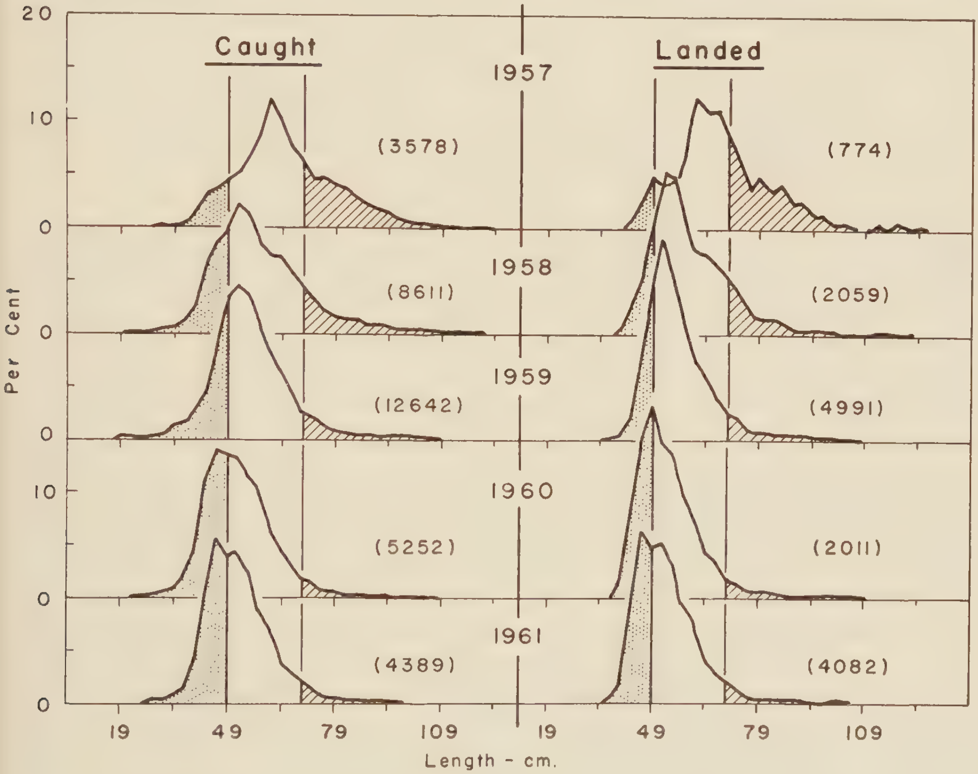

FIG. 8. Size compositions of cod caught and landed by northern New Brunswick draggers fishing in the southwestern Gulf of St. Lawrence with large-mesh (4½-inch) codends, 1957 to 1961.

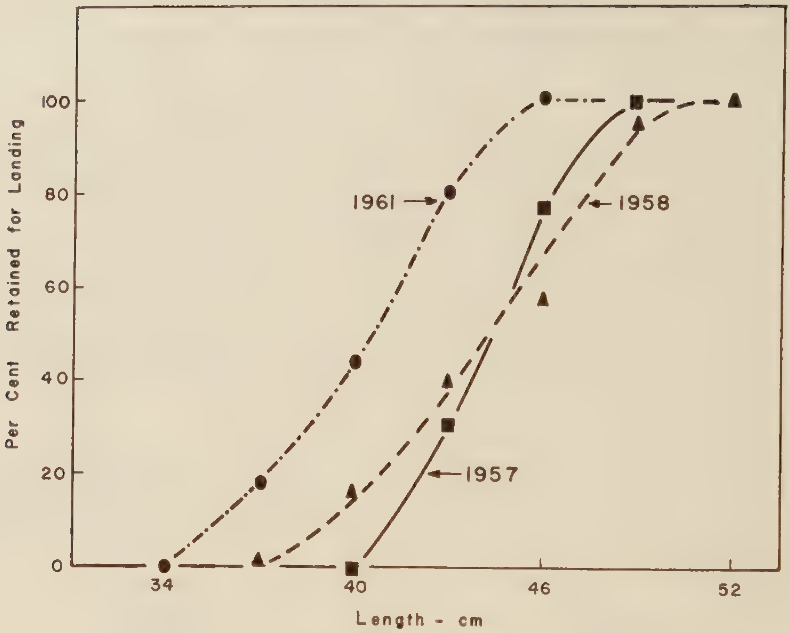

FIG. 9. Selection curves for landing (cull) based on sea and wharf samples from commercial draggers fishing in the southwestern Gulf of St. Lawrence with large-mesh codends (4½-inch), 1957 to 1961. The curves for 1959 and 1960, omitted from the graph, fall between the 1957 and 1961 curves.

mesh size and a reduction in cull size have played a major part in reducing cod discards in the southwestern Gulf of St. Lawrence in recent years (Table III). Of the other factors known to affect discards, area fished may be ruled out. There is no evidence from commercial log records that the northern New Brunswick fleet, when fishing in the southwestern Gulf, has recently been concentrating on different fishing grounds. The reduction in cod discards cannot be attributed to avoidance of concentrations of small cod.

An increase from 1957 to 1961 in the proportion of scrod in the catch (Fig. 8) would normally result in a greater percentage being discarded (Fig. 4). Obviously, the "scrod effect" has been masked by the more important mesh and cull effects, and discards have declined in spite of an increase in relative abundance of scrod in the catch.

Theoretical considerations, presented later, and based on 1961 data, suggest that the use of a 3-inch mesh in 1961 (Fig. 9) would have increased the ratio of number of scrod to total numbers caught from about 0.5 to 0.6. These ratios are much higher than the ones shown in Fig. 4. It is doubtful if in that range a difference of 10% in the relative abundance of scrod in the catch would affect discards measurably.

In the following discussion, the effect of abundance of scrod in the catch is considered to be negligible, at least in 1961.

Relative Effects of Mesh Size and Selection for Landing on Discards

To measure the relative effects on discards of an increase in mesh size and a decrease in sizes selected for landing, a theoretical catch curve for a 3-inch manila codend was derived from the 1961 survey catches. This was done by first comparing actual catch using 3-inch mesh with actual survey catches in 1957, the year when surveys with fine-mesh codends were started in the southwestern Gulf. The selection curve obtained was then applied to the 1961 survey catches on the assumption that the distribution of cod within the 3-inch mesh selection range did not differ appreciably during these two years.

To the theoretical 1961 small-mesh catch the large-cull (1956) and small-cull (1961) curves were applied, resulting in the landing curves shown in Fig. 10A and B. Discards were calculated by subtracting numbers landed from numbers caught. These represent the theoretical discards in 1961 had small-mesh codends been used and had the small and large culls been in effect. In the next step a large-cull curve was applied to the actual catch with large-mesh codends in 1961 (Fig. 10C), and discards were calculated. Fig. 10D shows the actual sizes landed with the large mesh and the small cull in effect in 1961. All frequencies were adjusted above 50 cm. The numbers of cod discarded (in brackets in Fig. 10) in each case are therefore comparable.

If A, B, C and D represent the numbers discarded with the various combinations of mesh and cull shown in Fig. 10, then:

A – C = reduction in discards due to mesh = 1,444 – 463 = 981
A – B = reduction in discards due to cull = 1,444 – 662 = 782
A – D = reduction in discards due to both mesh and cull = 1,444 – 126 = 1,318

These are relative numbers based on the numbers of fish sampled at the wharf.

The relation between mesh and cull effects may be expressed as the ratio:

$$\frac{981}{782} = 1.3$$

It is concluded that an increase in mesh size has contributed more toward reducing discards in 1961 than the selection of small sizes (cull) for landing, by a ratio of about 1.3 to 1.

Observations made in 1957, the first year of conversion to large-mesh nets (Martin and Jean, 1958), provided actual catch data with small- and large-mesh nets and landings with large cull. These data, when submitted to a similar analysis, show that in 1957 the mesh effect would have been about 1.5 times greater than the cull effect had the 1961 small cull been in effect that year.

Cod Discards by the New Brunswick Dragger Fleet

The total cod discards by the New Brunswick dragger fleet were estimated from the data collected on sampling trips from 1956 to 1960. (Total 1961 landings were not available at the time of writing.) Regular wharf sampling of the dragger landings provided yearly average weight per fish landed during these years. The total numbers landed were calculated from the total weights landed. Applying the discard figures listed in Table III to total weights and total numbers landed, the yearly total discards by the New Brunswick fleet were calculated (Table XII).

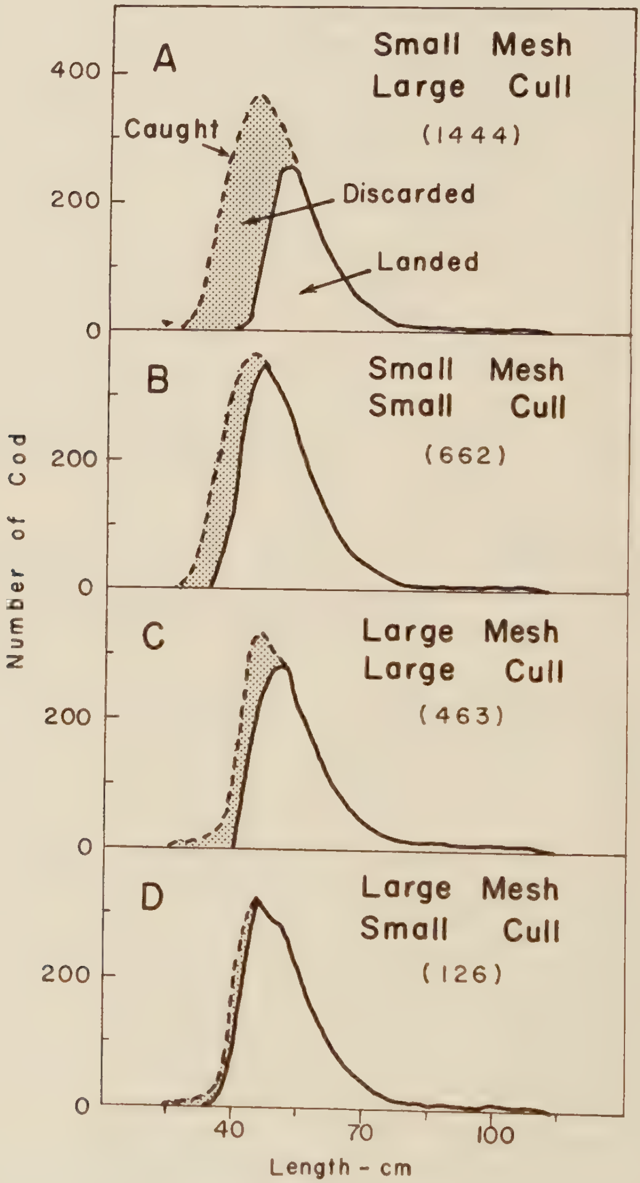

FIG. 10. Size compositions of cod caught and landed by northern New Brunswick draggers with various mesh and cull sizes. D is based on actual 1961 samplings; others are theoretical. Numbers discarded are in parentheses.

TABLE XII. Total cod discards by the northern New Brunswick dragger fleet from 1956 to 1960.

Year	Boats	Total weight landed	Av. weight per fish landed	Total no. landed	Discards By weight	Discards By number	Total discards By weight	Total discards By number
	no.	*million lb*	*lb*	*million*	*%*	*%*	*million lb*	*million*
1956	58	32.3	5.8	5.6	9	25	3.2	1.9
1957	59	30.4	5.5	5.5	6	24	1.9	1.7
1958	59	26.0	3.8	6.8	7	16	2.0	1.3
1959	62	30.6	2.9	10.5	6	13	2.0	1.6
1960	65	16.4	2.9	5.7	4	10	0.7	0.6

The total weight of cod discarded at sea by New Brunswick draggers has decreased from 3.2 million lb per year in 1956 to 0.7 in 1960. The total number discarded has decreased from 1.9 to 0.6 million per year during the same period.

The use of larger mesh and smaller retention length for landing has resulted in a reduction of about 75% by number and 65% by weight in the wastage of small cod at sea by northern New Brunswick draggers.

TOTAL COD DISCARDS IN THE SOUTHWESTERN GULF OF ST. LAWRENCE

Total cod discards in the southwestern Gulf of St. Lawrence may be estimated from total landings, using the discard percentages given in Table III, provided the following assumptions are correct. First, line fishermen do not discard cod at sea. Second, the discarding practices observed aboard northern New Brunswick draggers also apply to other small otter trawlers fishing in the southwestern Gulf in summer. Third, the European otter-trawl fleet fishing off the Cape Breton coast (Fig. 1) in the spring discard the same proportion of their catch as the northern New Brunswick draggers.

No observations are available on discards of small cod at sea by line fishermen. McCracken (1957) showed that the 50% retention length for cod by No. 14 hooks was about 48 cm. According to Jean and Marcotte (1959), the 50% selection length for No. 14 hooks may be as high as 53 cm. As seen in Fig. 9, almost all cod larger than 44 cm caught by draggers in 1961 were landed. Presumably the acceptable sizes for landing by draggers applied to lines as well. In such a case the number of fish smaller than 44 cm caught by lines would be quite small. This suggests that even in 1961, when the size of fish landed by lines (Table XIII) was lower than average and more likely to be discarded, all fish caught by lines were landed. Discards, if any, were negligible. In the following calculations it is assumed that line fishermen do not discard cod at sea.

Little is known of cod discards by draggers other than those operating from northern New Brunswick ports. During the period under study, two sampling trips were made on Gaspé draggers, one in July 1959 and the other in August 1961. The latter was a redfish trip and few cod were caught. Cod discards on the July 1959 trip were 1% by number and less than 1% by weight. At about the same time New Brunswick draggers were discarding 3% by number and 1% by weight of their catch. This comparison suggests that Quebec draggers may

TABLE XIII. Total weights and numbers of cod landed and discarded at sea in the southwestern Gulf of St. Lawrence, 1956 to 1961. (From ICNAF Statistical Bulletins; 1961 discards estimated.)

Year	1956	1957	1958	1959	1960	1961
Weight landed (millions of lb)						
Canadian, lines	71.1	76.1	64.7	59.0	43.2	...
Canadian, otter trawl	43.5	47.8	40.2	45.9	25.2	...
European, otter trawl	77.2	39.9	54.0	107.5	53.3	...
Total	191.8	163.8	158.9	212.4	121.7	...
Average weight per fish landed (lb)						
Lines	8.54	9.76	9.76	9.76	5.11	4.85
Otter trawl	5.82	5.47	3.78	2.92	2.89	2.65
Numbers landed (million of fish)						
Canadian, lines	8.3	7.8	6.6	6.0	8.5	...
Canadian, otter trawl	7.5	8.7	10.6	15.7	8.7	...
European, otter trawl	13.3	7.3	14.2	37.0	18.3	...
Total	29.1	23.8	31.4	58.7	35.5	...
Weight discarded (millions of lbs)						
Canadian, lines	Nil	Nil	Nil	Nil	Nil	Nil
Canadian, otter trawl	4.3	3.1	3.0	2.9	1.1	0.6
European, otter trawl	7.6	2.5	4.1	6.3	2.2	0.4
Total	11.9	5.6	7.1	9.2	3.3	1.0
Numbers discarded (millions of fish)						
Canadian, lines	Nil	Nil	Nil	Nil	Nil	Nil
Canadian, otter trawl	2.5	2.7	2.0	2.3	1.0	0.6
European, otter trawl	4.4	2.3	2.7	5.5	2.0	0.4
Total	6.9	5.0	4.7	7.8	3.0	1.0

discard a smaller proportion of their catch than the New Brunswick draggers. However, both sets of figures are estimates. For the purpose of this discussion it is assumed that there is no appreciable difference in discards by small otter trawlers fishing in the southwestern Gulf of St. Lawrence.

Finally, it is also assumed that cod discards by European trawlers fishing in Divisions 4T and 4V in the spring do not differ markedly in percentage and size from those of northern New Brunswick draggers. Clark and McCracken (1958) measured a sample of discards aboard a French trawler fishing off the Cape Breton coast in March 1958 (McCracken, 1958). The average length of these discards was 42.5 cm (ICNAF, 1959). The same authors estimated that about 10% by weight of the catch was discarded during that trip. Sampling trips in the southwestern Gulf during the summer of 1958 indicated that the mean length of cod discarded by New Brunswick draggers was 41.5 cm. The overall percentage discards of the New Brunswick draggers was 7%. These observations suggest no large differences in the sizes and percentages of the catch discarded by the two fleets. The discard data collected from northern New Brunswick draggers were therefore applied to European trawlers.

On the above assumptions, total cod discards were calculated from total landings from the southwestern Gulf of St. Lawrence (including the Cape Breton coast in the spring) during the years 1956 to 1960 (Table XIII). Discards for the year 1961 were estimated. The table shows that total discards by weight have decreased from about 12 million lb per year in 1956 to 3 million lb in 1960 and an estimated 1 million lb in 1961. Discards by numbers have been reduced from about 7 million fish in 1956 to 3 million in 1960 and an estimated 1 million in 1961. These figures suggest that about 6 million fish which would have been discarded in 1956 were either released by a larger mesh or caught and landed in 1961. It was estimated that the mesh effect was 1.3 times that of cull effect in reducing cod discards in 1961. This would indicate that from 1956 to 1961 large-mesh codends were responsible for a reduction in discards of about 3.5 million fish in numbers in the southwestern Gulf of St. Lawrence. A further reduction of 2.5 million fish resulted from the smaller cull size for landing.

IMMEDIATE EFFECTS OF 5- AND 5½-INCH MESH ON CATCH, DISCARDS AND LANDINGS

Beginning in 1959 nylon and other synthetic fibres replaced manila in the codends and cotton in the body of the nets used by northern New Brunswick draggers. In 1961 nearly all nets were of synthetic fibres, such as nylon, terylene, courlene, anzalon, etc. Even with synthetic fibres, the codends had a mesh size of about 4½ inches, equivalent to about 5 inches (127 mm) manila (Clark *et al.* 1958), i.e., about ½-inch larger than the regulation mesh.

In order to evaluate the effects of 5- and 5½-inch (140 mm) mesh (manila equivalent) on catch, discards and landings of cod, the selection curves for these mesh sizes were plotted against the 1961 selection curve for landings (Fig. 11). A selection factor:

$$\frac{\text{50\% retention length}}{\text{mesh size}}$$

of 3.5 for manila and 3.8 for synthetics (Clark *et al.* 1958) was used in calculating the 25, 50 and 75% retention lengths of 5- and 5½-inch mesh manila codends.

The immediate effect of 5-inch (manila equivalent) mesh, as discussed earlier, has been a reduction in discards by about 3.5 million cod in the southwestern Gulf of St. Lawrence between the years 1956 and 1961. Another immediate effect has been the release of some cod which normally would have been landed (Fig. 11). Presumably some of these released fish were caught again and landed after growing to a larger size.

A more efficient fishing operation resulting from a 5-inch mesh may more than compensate for the temporary loss of cod of marketable size. Firstly, the release of small unmarketable fish and other trash reduces work on deck and contributes toward a more rapid operation. Secondly, as shown by Graham and Premetz (1955) and Clark and Nechy (1957a, 1957b) for Georges Bank haddock, large-mesh nets are more efficient in catching large fish. Because of inadequate catch statistics prior to mesh regulation, the effect of large-mesh nets on total cod

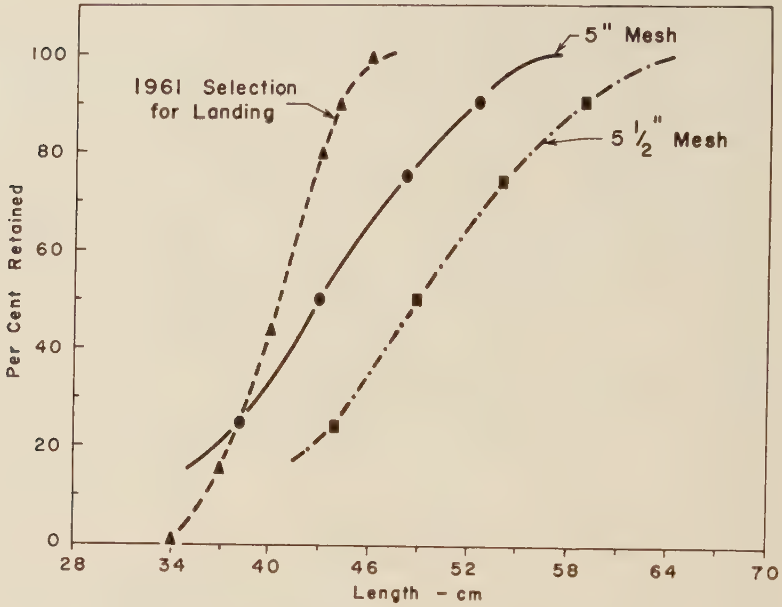

FIG. 11. Selection curves for cod of 5- and 5½-inch manila codends plotted against the 1961 selection curve for landing.

landings in the southwestern Gulf of St. Lawrence is difficult to measure, especially if the increase is of the same order (5%) as the one observed for haddock. Martin and Jean (1958) could not detect any reduced landings per trip in northern New Brunswick draggers which had adopted the regulation mesh in 1957.

From statistics and sampling data collected from commercial and research vessels, the ICNAF Working Group of Scientists on Fishery Assessment in Relation to Regulation Problems (1962) evaluated the long-term benefits of large-mesh nets in the Convention Area. They estimated that use of 5-inch mesh nets in the southwestern Gulf of St. Lawrence would result in a 2% to 4% increase over the 1956 and 1958 cod landings by all gears.

The immediate effects of 5½-inch mesh would be a further reduction and possibly complete elimination of discards (Fig. 11). It would also release a larger quantity of marketable cod. The long-term effect, on the other hand, would be a greater benefit than the one caused by 5-inch mesh, according to the ICNAF Working Group just cited. They estimated that 5½-inch mesh would eventually increase weights of cod landed by 3% to 8% over those of 1956 and 1958 in the southwestern Gulf of St. Lawrence.

SUMMARY

1. This study is based on 44 sampling trips from 1956 to 1961 aboard commercial draggers fishing in the southwestern Gulf of St. Lawrence, mainly from northern New Brunswick ports.
2. Important factors affecting cod discards at sea are: codend mesh size, relative abundance of small fish in the catch, area fished and sizes selected for landing.

3. From 1956 to 1961 cod discards in the southwestern Gulf of St. Lawrence have been reduced from 25% to 6% by numbers and from 9% to 6% by weight.
4. Two factors are mainly responsible for the reduction in cod discards: large-mesh nets which, following an ICNAF recommendation, became effective in 1957, and reduction in sizes retained for landing (cull). The mesh effect is believed to be about 1.3 times greater than the cull effect in the reduction of discards in 1961.
5. These results were applied to the southwestern Gulf fishery as a whole. It is estimated that total discards of cod have been reduced by about 6 million fish, from 7 million per year in 1956 to 1 million in 1961. An increase in mesh size is believed to be responsible for a 3.5 million reduction. The decrease in sizes selected for landing resulted in a further reduction of 2.5 million in the numbers of fish discarded.
6. Log-book estimates indicate that, in contrast to cod, plaice discards have increased from about 17 to about 50% by weight in recent years. This is due to an increase in the abundance of small fish in the catch.
7. The discards of incidental species in the southwestern Gulf are considered to be unimportant since these species are a small part of the catch.
8. Experiments carried out on a research vessel indicate that cod and plaice are dead when discarded.
9. The use of 5-inch mesh nets (manila equivalent), besides reducing discards, has released some fish of marketable size. Increase in fishing efficiency, although difficult to measure, may compensate for the temporary loss. The long-term benefits have been estimated as a 2% to 4% increase in total cod landings by all gears. A 5½-inch mesh would eliminate cod discards. It would also release a larger quantity of cod of marketable size. The long-term benefits are estimated to be an increase of 3% to 8% in the total cod landings over those of 1956 and 1958 in the southwestern Gulf of St. Lawrence.

ACKNOWLEDGMENTS

The author wishes to acknowledge the help of summer assistants, P. M. Powles, L. L. MacLeod, W. E. Russell, R. M. Sutherland and I. R. Woolfrey, who collected wastage data at sea during the years 1956 to 1961, and of D. N. Fitzgerald who assisted these observers in their work ashore. I would like to thank all the captains who have taken observers aboard their draggers for one or more sea trips, and also those who, on several occasions, have provided accurate counts of their cod discards at sea. Sincere thanks are due to Dr W. R. Martin for his advice throughout this investigation, his supervision of the survival experiments and his help in preparing this paper. I wish to thank Dr F. D. McCracken and Mr L. R. Day who read the manuscript and offered helpful suggestions and criticisms. Two sampling trips on Gaspé draggers were arranged through Dr A. Marcotte, Director of the Marine Biological Station at Grande-Rivière, Qué. His co-operation is much appreciated.

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Note: ICNAF = International Commission for the Northwest Atlantic Fisheries.

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Some Effects of Simultaneous Variation in Salinity, Temperature and Dissolved Oxygen on the Resistance of Young Coho Salmon to A Toxic Substance[1]

By D. F. Alderdice

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Median resistance times of juvenile coho salmon (*Oncorhynchus kisutch*) acclimated to fresh water at 12°C were investigated at 3 mg/l of sodium pentachlorophenate over combinations of levels of salinity, temperature and dissolved oxygen using factorial schemes developed by Box and associates. For the relationship:

$$\zeta = \varphi(x_1, x_2, x_3, \ldots, x_k)$$

a true response ζ is regarded as a function of combinations of levels of k quantitative factors $x_1, x_2, x_3, \ldots, x_k$. The relationship was approximated by a polynomial in x for the three coded factors—salinity (x_1), ‰; temperature (x_2), °C; and dissolved oxygen (x_3), mg/l. The experimental data were fitted to a second-order polynomial:

$$Y = 59.9319 + 9.5469x_1 - 10.8943x_2 + 0.1746x_3 - 2.2690x_1^2 - 4.4291x_2^2$$
$$- 4.0143x_3^2 - 1.2360x_1x_2 + 2.5328x_1x_3 - 0.2671x_2x_3$$

This was transformed to its canonical form, from which ellipsoidal response surfaces were constructed. Alternative levels of salinity, temperature and dissolved oxygen were computed for general evaluation of the manner in which these variables altered the response to the pentachlorophenate. A maximum response time was computed for the response surfaces, associated with levels of the three variables at 17.68‰ salinity, 4.86°C and 7.66 mg/l, O_2.

The use of multivariable experimental techniques is discussed as a means of considering the significance of alteration in the levels of associated environmental factors in evaluation of experimental or environmental situations involving water quality alteration.

INTRODUCTION

General Concepts

The history of examining the ability of animals to tolerate the physical and chemical aspects of their environment has been one of growing complexity. This growth has been natural, progressing from the idea of a single end *point* such as a lethal temperature, to a *range* of lethal temperatures influenced by temperature pre-experience. Since temperature may be lethal at both upper and lower levels the range took on the form of an *area* of response which Fry (1947) termed the zone of tolerance. Zones of tolerance may be determined individually for any number of factors. As far as temperature is concerned, *per se*, the picture may be considered as reasonably complete for a number

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[1] Received for publication February 19, 1962.

[2] Paper No. 7 concerning the physiology and behaviour of salmonid fishes from the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.

J. Fish. Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

of species. However, such an assumption must be tested and cannot be accepted *a priori*, for the experimenter may purposefully or inadvertently accept variation in the presence, or constraint in the levels, of many other variables in the course of testing. Thus, dissolved oxygen levels may be maintained at "adequate" levels by aeration, pH may be measured or frequently neglected, and characteristics of water such as hardness, although often omitted, have more recently been listed although, in many instances, without specific knowledge of their possible effect. Such factors as these could have significance in the definition of chances for survival in nature. Persistent questions with regard to the acceptable levels of toxic materials in water require an experimental approach which takes into account the whole domain of environmental factors which normally prevails as a multivariable system.

It should be noted that within the zone of tolerance for a given factor no area of maximum survival time or minimum stress could be set other than by selection of another response than death, such as growth, activity, efficiency of food conversion, or by compressing the survival area through extension of one or more of the ancillary variables to the point where their levels directly interfere with survival.

By selection of a lethal stressor, however, the area within a tolerance domain may be compressed to the point of removal, since at no point could the animal be expected to live indefinitely. In this way measures of mortality can be retained as a means for determining optimal survival terms within a set of chosen variables. If these chosen variables are progressively expanded to encompass all possible variates, then theoretically circumstances in nature have been realized.

The point response has been considered in terms of its expansion to an area or zone of tolerance. It is now proposed to investigate response surfaces enclosing a tolerance *solid* through the imposition of a lethal stressor over multiple zones of tolerance. Simplicity, therefore, gives way to complexity. The complexity is inevitable, no matter how inconvenient it may be to one of the major tasks at hand—the determination of effects of toxic materials in nature.

Experimental Considerations

The reaction of an animal with respect to a stimulus is dependent for its expression on many circumstances, such as species, age or size, the response chosen for measurement and the conditions to which the animal was exposed prior to the stimulus.

The relationships existing between a response and variables which may relate to pre-test conditions are becoming increasingly well documented (Fry, 1947; Prosser and Brown, 1961) as, for example, in the case of temperature (Brett, 1952), oxygen supply (Shepard, 1955; Job, 1955), salinity (V. S. Black, 1951, 1957; McLeese, 1956; Baggerman, 1960), carbon dioxide (E. C. Black *et al.*, 1954; Basu, 1959), and activity (E. C. Black, 1957, 1958). The knowledge that variation in such conditions, prior to utilization of test animals, may have a marked effect on the estimate of response to test conditions is now widely appreciated.

As a characteristic of the stimulus, the median effective time to death is a widely employed measure of response, although other *quantitative* (Finney, 1952) measures of response time are used (see Wuhrmann, 1952). In general, the fishery investigator tends to avoid measuring other possible quantitative properties of the test animal although they may be very useful (see Neil, 1957).

Another fundamental source of variation in the definition of response is that arising from the presence of unappreciated or uncontrolled variables in the domain examined. From this category of error may arise a dissimilarity of estimates provided by various laboratories. It is probable that geographical differences in the nature of water supplies could be a major contributor in this regard. Response estimates may in this manner be associated with differences in pH, total hardness, and variations in the kind and quantity of naturally occurring anions and cations (Doudoroff, 1956; Doudoroff and Katz, 1950, 1953).

Although standardization of experimental tests around one species at one age or size and consideration of one response system for selected pre-treatment conditions could undoubtedly improve the reproducibility of an estimate of effect, the result would be one constrained to apply to only limited conditions in a large field of possibilities. When an investigator is faced with a practical problem in water quality alteration, a prevailing tendency is that of attempting to provide an estimate representing the maximum alteration which may be permitted in terms of a particular additive or change. Moreover, the estimate is derived by consideration of a response of fish of a particular species and age, selected not so much on the basis of requirements for standardization, but because of its availability or association with the situation examined.

Since there are valid practical reasons for wishing to investigate a particular species with respect to its response to a specific situation it seems desirable to accept the fact that a number of species of fishes will be involved in determinations of water quality. It follows that the definition of specific test conditions should be made with a knowledge of the effect of a number of ancillary variables on the animal in question. However, it often occurs that the simultaneous operation of such variables on a response system is that about which information is required. The simultaneous operation of several or more variables produces a considerable increase in the complexity of experimental procedures. This complexity has perhaps tended to limit to some extent the consideration of multivariable phenomena.

In view of the problems outlined, it is proposed to consider a multivariable system utilizing methods of analysis proposed by Box and associates (Box and Wilson, 1951; Box, 1954, 1956), as they may be applied to biological assay problems in fisheries technology. The advantages implied in this proposal are twofold. There is an advantage to be gained in the examination of toxic or pollutional factors with simultaneous consideration of other variables which may enter the system and modify the response measured. Instances of such modification are well known in the effect of synthetic detergents on oxygen consumption (Herbert *et al.*, 1957), the effect upon toxicity of un-ionized ammonia of the presence of carbon dioxide (Lloyd and Herbert, 1960) and of low dissolved oxygen levels (Downing and Merkens, 1955; Merkens and Downing, 1957), the influence of temperature on survival at low oxygen tensions (Downing and Merkens, 1957; Davidson *et al.*, 1959), the relationship between carbon dioxide level and oxygen utilization (Alabaster *et al.*, 1957) and the influence of dissolved oxygen concentration on the toxicity of cyanide (Downing, 1954) and of various other poisons (Lloyd, 1961). In addition, the method may prove useful in examining the influence of ancillary variables on quantitative measures of other response systems having to do more with variations in performance, such as swimming speed, than with viability.

It is considered necessary to reaffirm the fact that the environment is not usually a simple system. Single-factor analyses of the response of fishes to an environmental variable will provide insight into unique functional abilities of the animal. Knowledge of the extent to which these abilities may be utilized may be gained by appreciation of the manner in which the response may be altered over the various levels of factors to which, at one time or another, the animal may be exposed.

MATERIALS AND METHODS

Of primary concern in this study was the examination of potential variation in the viability of test animals exposed to several levels of salinity, temperature and oxygen supply. Since it was desirable to consider these as auxiliary variables contributing to a state of stress in the test animals while not in themselves eliciting the response, the range over which each of the three factors was allowed to vary at selected levels was maintained within the zone of tolerance for each factor. In order to operate within short enough time periods, a primary acute stressor was imposed on the auxiliary system. In selecting the primary stressor a number of toxic chemicals was screened to select one of high water solubility, high toxicity, presumed non-specific toxic action and availability as a dry product of high purity and stability. Sodium pentachlorophenate was selected, being made up periodically from the pentachlorophenol. Response-time distributions were investigated at acute levels of the pentachlorophenate and a concentration of 3 mg/l was selected to act as the primary stressor. Estimates of median response time were obtained as scaled from the provisional log-time probit-mortality distribution (Bliss and Stevens, 1937) in each test. The system measured then becomes one of variation in stress imposed on the test animals by a system of auxiliary variables operating on the response to a particular toxic material.

The variables were selected on the basis of their importance in the environment of the test animal selected for the study, young coho salmon (*Oncorhynchus kisutch*). Test fish were collected as juveniles from several streams in the vicinity of the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C., in September, 1960, and were cultured in fresh water for a period of 9 months prior to their use as smolts. The experimental fish had lived approximately 16 months since emerging from the gravel, probably in March, and averaged 11.51 cm fork length and 15.44 g in weight. Prior to testing, experimental fish were held in an acclimation tank of aerated, circulating, flowing fresh water at 12°C for a period at least equal in days to the number of degrees

Centigrade difference between the temperatures of culturing and acclimation. Tests were conducted on samples of 10 fish in 35 litres of water. Selection of fish for the various tests run concurrently were made by consulting tables of random numbers.

Temperature control in the tests was maintained within ±0.05°C. Various salinities were obtained by dilution of sea water with fresh water with adjustment to ±0.05‰ S (salinity) by the Mohr method. Oxygen concentrations were maintained by mixing various proportions of compressed air and nitrogen gas supplied from cylinders through back-pressure compensated regulators to each of two gangs of oxygen flowmeters mounted on manifolds maintained at a constant pressure of 20 pounds per square inch (1.4 atmospheres above atmospheric pressure). Gases metered from the two supplies were mixed in a gang of acetylene torch mixers and supplied to Alundum aerators in each tank at a total, constant gas flow of 17 cubic feet (0.48 cu m) per hour. Circulation of the tank contents by the gas supply ensured against thermal stratification in the test tanks. Required oxygen partial pressures were calculated initially on the basis of relationships provided by Gameson and Robertson (1955) and Truesdale and Gameson (1957) for obtaining saturation levels at various temperatures and salinities. Final adjustments to the gas proportions were made to provide dissolved oxygen concentrations within ±0.05 mg/l of those required, as measured by unmodified Winkler titration of the test solutions before the addition of

TABLE I. Orthogonal composite factorial design for the 3 factors at 2 levels (columns 2–4). Columns 5 and 6 show the response, Y (the median resistance time in minutes for samples of 10 fish), for each of two replicates of each trial. All trials were conducted in a concentration of 3 mg/l of sodium pentachlorophenate. (See text for details.)

1	2	3	4	5	6
	Coded factor level			Response, Y	
Trial	x_1	x_2	x_3	Rep 1	Rep 2
				min.	*min.*
1	−1	−1	−1	53	50
2	−1	−1	1	54	42
3	−1	1	−1	40	31
4	−1	1	1	37	28
5	1	−1	−1	84	57
6	1	−1	1	76	78
7	1	1	−1	40	49
8	1	1	1	50	54
9	0	0	0	50	50
10	1.215	0	0	61	76
11	−1.215	0	0	54	45
12	0	1.215	0	39	33
13	0	−1.215	0	67	54
14	0	0	1.215	44	45
15	0	0	−1.215	61	38

sodium pentachlorophenate. In some of the tests conducted with temperatures near 0°C, the low temperatures were established by circulating refrigerated ethylene glycol through coils in the test compartments. pH was monitored by Beckman glass electrode before and after each test with variation in pH seldom exceeding ±0.05 units. Pentachlorophenate concentrations were checked by a modification of a procedure outlined by Haskins (1951).

The experimental design upon which this study is based is one of a group of (2^2, 2^3, . . ., 2^k, . . ., 2^n) full or fractional factorial designs, which may have added to them a series of $2k + 1$ axial points. The one used is a full 2^3 design which will estimate all of the linear effects and linear × linear interactions. The $2k + 1$ axial points were included for the estimation of quadratic effects. A composite design of this sort compares favourably with a 3^3 design when the precision of estimates from the composite design is weighed against the larger number of experiments required for the 3^3 factorial. Values of the axial points, ±1.215, are chosen so that covariance elements of the sub-matrix of quadratic effects in $(\mathbf{X}'\mathbf{X})^{-1}$ are zero (see Appendices A, B; Box and Wilson, 1951, Appendix 4). A more complete survey of designs of this type may be found by consulting Box and Wilson (1951) and Davies (1956, chapters 7–11).

RESULTS

Tests were conducted on the basis of 2 replications of the 15-trial orthogonal composite design indicated. Levels of the variables (Table I) are coded as follows:

Coded variable	Factor	Levels			Base level	Unit
x_1	Salinity, ‰ S	9	5	1	5	4
x_2	Temperature, °C	13	10	7	10	3
x_3	Dissolved oxygen, mg/l	7.5	5.5	3.5	5.5	2

The coded values of the factors are found as follows:

$$x = \frac{\text{factor} - \text{base level}}{\text{unit}}$$

For example, the coded values of the above three salinity levels are:

$$x_1 = \frac{S - 5}{4}$$

where S represents each of the three salinity levels.

The proposition is now advanced that a true response η which is dependent on the combinations of levels of k controlled quantitative factors $x_1, x_2, \ldots, x_k$ may be stated for the u^{th} combination as:

$$\eta_u = \varphi(x_{1u}, x_{2u}, \ldots, x_{ku})$$

where $u = 1 \ldots N$ (Box and Wilson, 1951). The observed response Y_u is an estimate of η_u and will have variance σ^2 measured by s^2.

It is assumed that in the k-dimensional factor space there will be a region limited by upper and lower incipient lethal levels of the variables in question and that within this region there will be a point or points at which the response will be maximal. It is also assumed that this response centre will be bounded by regions of equal but sub-maximal response. Evaluation of the configuration of the domain should allow estimation of the relative effects of the various levels of the several factors on the response in terms of a measure of viability within the domain.

The response function may be approximated by the polynomial

$$z = \beta_0 x_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_{11} x_1^2 + \beta_{22} x_2^2 + \beta_{33} x_3^2 + \beta_{12} x_1 x_2 + \beta_{13} x_1 x_3 + \beta_{23} x_2 x_3$$

for 3 factors, assuming that cubic effects may be safely ignored. In the polynomial the dummy variable x_0 is introduced as a convenience. Its value is unity and $\beta_0 = \beta_0 x_0$. Preliminary trials suggested that cubic effects could be ignored within the experimental region selected.

Analysis of variance of the 2 replicates of trials from Table I is illustrated in Table II (see also Appendix A).

The ratio of the mean square for deviations from regression and the mean square for experimental error provides an estimate of the goodness of fit of the data to the second-degree equation. Since the deviations mean square is smaller than the experimental error mean square there is no evidence suggesting the need for higher order terms in the equation (Box, 1956). The second-order polynomial is considered as an adequate representation of the data in the factor space investigated.

Estimates $b_0, b_1, b_2, \ldots$ of $\beta_0, \beta_1, \beta_2, \ldots$ are now obtained with their standard errors (Appendix B).

$$\begin{array}{lll}
 & b_0 = 51.0867 \pm 5.216 & \\
b_1 = 9.0469 \pm 2.395 & b_{11} = 5.4581 \pm 3.796 & b_{12} = -2.5000 \pm 2.803 \\
b_2 = -10.2603 \pm 2.395 & b_{22} = -1.9932 \pm 3.796 & b_{13} = 2.5000 \pm 2.803 \\
b_3 = -0.0068 \pm 2.395 & b_{33} = -2.6706 \pm 2.796 & b_{23} = 0.2500 \pm 2.803
\end{array}$$

Hence:

$$Y = 51.0867 + 9.0469x_1 - 10.2603x_2 - 0.0068x_3 + 5.4581x_1^2 - 1.9932x_2^2 - 2.6706x_3^2 - 2.5000x_1x_2 + 2.5000x_1x_3 + 0.2500x_2x_3$$

An estimate of the location of the centre of the response domain may now be obtained from the "path of steepest ascent to a near-stationary region" (Box, 1956). When the quadratic effects indicate that the amount of curvature associated with the planes related to b_1, b_2 and b_3 over the experimental range is not too large, the relative magnitude of the slopes b_1, b_2 and b_3 and their signs provide a series of planes in a conic configuration. A stepwise procedure will allow progression up the slopes to a near-stationary region of response. Since quadratic effects will assume more and more importance as the near-stationary region is approached, estimates of its position in terms of the linear effects will provide at best an approximation of the point (or points) of maximum response.

TABLE II. Analysis of variance of the data from Table I.

Source of variation	Sum of squares	Degrees of freedom	Mean square
Total	84864.00	30	
Fitting β_0	79053.33	1	
Remainder	5810.67	29	
Replicates	213.3	1	
Treatments	4717.7	14	
Fitting $\beta_1 \ldots \beta_{23}$	4663.05	9	
Deviations from regression	54.65	5	10.93
Reps × Treatments (exptl. error)	879.7	14	62.84

An estimate of the region of stationary response was obtained from responses observed in a new sequence of trials, the loci of these trials being computed from the data in Table III.

Response times obtained with the new sequence of trials indicate that a region of maximum response occurs in the vicinity of 12‰ S, 4°C and 5.5 mg/l O_2.

The second-degree equation yields estimates of the response which would be obtained under the experimental conditions imposed within the range of the variables studied. The approximate location of a centre of maximum response has been obtained. Since the centre of the design (5‰ S, 10°C, 5.5 mg/l O_2) does not correspond with the approximated centre of maximum response it may be inferred that there will be another set of co-ordinates which will have the centre of the response surfaces at the centre of the new set of co-ordinates. Although

TABLE III. Calculation of a new series of experimental levels of salinity, temperature and dissolved oxygen by the "method of steepest ascent", to provide a sequence of trials through the region of near-stationary response.

	Salinity	Temperature	Oxygen	Y
Base level	5.0‰	10.0°C	5.5 mg/l	. . .
Unit	4	3	2	. . .
Estimated slope, b	9.05	−10.26	−0.007	. . .
Unit × b	36.20	−30.78	−0.014	. . .
Change per 1°C change in x_2	1.176	− 1.0	−0.0004	. . .
	‰	°C	*mg/l*	*min*
Path of steepest ascent,	5	10	5.5	50
beginning at the	6.18	9	5.5	. . .
centre of the design	7.35	8	5.5	71
	8.53	7	5.5	68
The responses observed	9.70	6	5.5	78
at these loci are shown	10.88	5	5.5	93
in the last column to	12.06	4	5.5	96
the right	13.23	3	5.5	66
	14.41	2	5.5	43

estimates of response may be obtained from the fitted polynomial, it is convenient to transform the polynomial to its geometric equivalent or "canonical" form (see Lanczos, 1956):

$$Y - Y_S = \lambda_{11}X_1^2 + \lambda_{22}X_2^2 + \lambda_{33}X_3^2$$

where Y_S = response at the centre or stationary region of the response configuration

λ_{ii} = the rate at which Y changes in moving away from the point S in the direction of the new X_i axes.

Initially, S, the stationary point, was found by partial differentiation of the computed polynomial with respect to x_1, x_2 and x_3, equating the derivatives to zero, and solving for the x's (Appendix C). The stationary point is calculated to be:

$$x_{1S} = -1.12437 \qquad x_{2S} = -1.90752 \qquad x_{3S} = -0.6169$$

Converting to original units:

$$S = 0.503‰ \qquad T = 4.277°\text{C} \qquad O_2 = 4.266 \text{ mg/l}$$

The response at S is now determined:

$$\begin{aligned} Y_S &= b_0 + \tfrac{1}{2}b_1x_{1S} + \tfrac{1}{2}b_2x_{2S} + \tfrac{1}{2}b_3x_{3S} \\ &= 55.79 \text{ minutes.} \end{aligned}$$

Some experimental determinations of Y have already exceeded Y_S. The salinity value estimated (0.503‰) at S is also lower than that suggested from the previous trials (12‰). It is suspected that the position of maximum response is remote from S as computed, that a local maximum has been found (a "col": Box, 1956), and that a ridge system is involved in the response configuration. Plotting of the observed responses to salinity at various temperatures, to salinities at various oxygen levels, and to temperature at various oxygen levels, indicates that response maxima occur for dissolved oxygen and temperature within or close to the region bounded by the experimental design. However, responses governed by salinity are shown to increase beyond the limits of the design. Evidently, a ridge system occurs with respect to salinity.

Determinations of the λ coefficients or eigenvalues in the canonical equation are now obtained by solution of the "characteristic equation" obtained from the determinant of quadratic and interaction terms of the discriminating cubic. Expansion of the determinant of order n provides a polynomial of order n in λ (Appendix D). Thus, where:

$$f(\lambda) = (-1)^3 \begin{vmatrix} b_{11}-\lambda & \tfrac{1}{2}b_{12} & \tfrac{1}{2}b_{13} \\ \tfrac{1}{2}b_{12} & b_{22}-\lambda & \tfrac{1}{2}b_{23} \\ \tfrac{1}{2}b_{13} & \tfrac{1}{2}b_{23} & b_{33}-\lambda \end{vmatrix} = 0$$

whence:

$$\lambda^3 + 25.7243\lambda^2 + 190.027999\lambda + 408.640160 = 0$$

and the roots or eigenvalues are:

$$\lambda_{11} = 5.8356 \qquad \lambda_{22} = -2.0648 \qquad \lambda_{33} = -2.9766$$

Hence:

$$Y - 55.79 = 5.8356X_1^2 - 2.0648X_2^2 - 2.9766X_3^2$$

Since λ measures the change in response in the direction of X, it follows that *S* is a maximum for X_2 and X_3 but that increases in response will be obtained remote from *S* in the direction of X_1. The response configuration is recognized as a system in which the contour surfaces are elliptical hyperboloids. Evidence to this effect was obtained from the sequence of trials performed on the path of steepest ascent (Table III). Further examination of the response surfaces was undertaken by trials in the direction of X_1 as listed in Table IV along with trials selected from Table III (trials 22–25).

TABLE IV. Responses observed in additional trials (to those of Table I) conducted for improved definition of the centre, S, of the response configuration (see Appendix E). Trials 22–25 are part of the series in Table III, their loci judged to be in the vicinity of S.

	Coded factor level			
Trial	x_1	x_2	x_3	Y
				min.
16	−1.2500	−1.8867	−0.6350	46
17	0.8600	−2.2200	−0.4250	66
18	1.0000	−2.2400	−0.3100	68
19	2.1165	−2.4167	−0.1450	75
20	2.5825	−2.4900	−0.0800	75
21	3.2475	−2.6667	0.0800	68
22	1.1760	−1.3333	0	78
23	1.4700	−1.6667	0	93
24	1.7640	−2.0000	0	96
25	2.0580	−2.3333	0	66

On the basis of all 25 trials of Tables I and IV the constants were recalculated with their standard errors (Appendix E):

$$b_0 = 59.9319 \pm 3.941$$

$$b_1 = 9.5469 \pm 2.385 \qquad b_{11} = -2.2690 \pm 1.617 \qquad b_{12} = -1.2360 \pm 1.877$$

$$b_2 = -10.8943 \pm 2.349 \qquad b_{22} = -4.4291 \pm 1.926 \qquad b_{13} = 2.5328 \pm 2.930$$

$$b_3 = 0.1746 \pm 2.559 \qquad b_{33} = -4.0143 \pm 3.871 \qquad b_{23} = -0.2671 \pm 2.911$$

The adjusted approximation to the stationary point *S*:

$$x_{1S} = 3.16998 \qquad x_{2S} = -1.70469 \qquad x_{3S} = 1.07849$$

Converting to original units:

$$S = 17.68‰ \qquad T = 4.86°C \qquad O_2 = 7.66 \text{ mg/l}$$

The roots or eigenvalues are:

$$\lambda_{11} = -1.4776 \qquad \lambda_{22} = -4.4403 \qquad \lambda_{33} = -4.7945$$

and $Y_S = 84.44$. Hence:

$$Y - 84.44 = -1.4776X_1^2 - 4.4403X_2^2 - 4.7945X_3^2$$

and the response configuration is ellipsoidal with centre at *S* (Fig. 1).

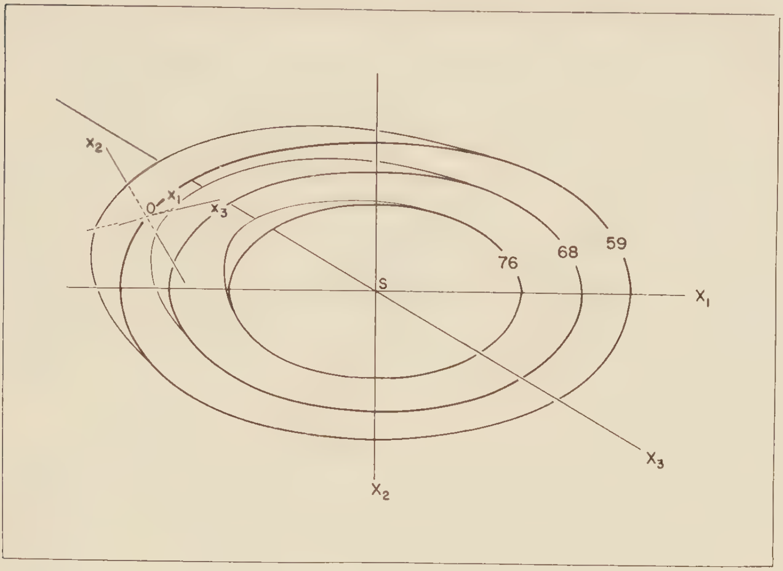

FIG. 1. Illustration of the ellipsoidal configuration of the response surfaces. The X-axes are those of the response surfaces, with centre *S*; the x-axes with centre *O* refer to the experimental factor space and its location with respect to the response surfaces. The figure was set up by constructing planes in X_1 and X_2 at intervals on the X_3-axis and sectioning in the X_1 and X_2 plane at $X_3 = 0$. The ellipsoids labelled 76, 68 and 59 refer to envelopes of 90, 80 and 70 per cent, respectively, of the maximum response time in minutes, computed for *S*.

Finally, the transformation of axes from those of the factor space to those of the response configuration is to be orthogonal, the centre *O* of the factor space being shifted to correspond with that of the response configuration, *S*, the axes being rotated and translocated but remaining at right angles to each other. Associated with each root or eigenvalue λ is a vector whose elements satisfy the requirements for axis transformation (Appendix F). These eigenvectors are, for each λ:

λ_{11}	λ_{22}	λ_{33}
m_1	m_2	m_3
0.87182	− 0.11147	− 0.47696
− 0.20271	0.80433	− 0.55856
0.44590	0.58362	0.67860

Hence:

$$\begin{aligned}
X_1 &= 0.87182(x_1 - x_{1S}) - 0.20271(x_2 - x_{2S}) + 0.44590(x_3 - x_{3S}) \\
X_2 &= -0.11147(x_1 - x_{1S}) + 0.80433(x_2 - x_{2S}) + 0.58362(x_3 - x_{3S}) \\
X_3 &= -0.47696(x_1 - x_{1S}) - 0.55856(x_2 - x_{2S}) + 0.67860(x_3 - x_{3S})
\end{aligned}$$

and since the transformation is orthogonal:

$$
\begin{aligned}
(x_1 - x_{1S}) &= 0.87182X_1 - 0.11147X_2 - 0.47696X_3 \\
(x_2 - x_{2S}) &= -0.20271X_1 + 0.80433X_2 - 0.55856X_3 \\
(x_3 - x_{3S}) &= 0.44590X_1 + 0.58362X_2 + 0.67860X_3
\end{aligned}
$$

Sets of computed alternative levels of salinity, temperature and dissolved oxygen providing 90% of the computed maximum resistance time of the test fish to 3 mg/l of the pentachlorophenate are listed in Table V.

The location of the loci from Table V on the axes of the response domain is illustrated in Fig. 2. The relationship of the axes of the response surfaces to those of the original factor space, translocated (but not rotated) so that the centre of the experimental factor space, *O*, corresponds with the centre of the domain, *S*, provides visual evidence of the interaction effects.

TABLE V. Alternative computed sets of levels of salinity, temperature and dissolved oxygen providing 90% of the response at the computed optimum. Each line shows a set of levels representing loci on the 90% of maximum response envelope of the response ellipsoid with centre *S*. The sets are derived by substitution of appropriate values for two of the X-axes, solution for the third in the canonical equation with $Y = 0.9Y_S$, transformation to the equivalents in x, and decoding to the original variables.

X_1	X_2	X_3	x_1	x_2	x_3	S	T	O_2
						‰	°C	*Mg/l*
0	1.378	0	3.0163	−0.5964	1.8827	17.07	8.21	9.27
0	−1.378	0	3.3237	−2.8130	0.2743	18.29	1.56	6.05
0	0	1.326	2.5375	−2.4454	1.9783	15.15	2.66	9.46
0	0	−1.326	3.8025	−0.9640	0.1787	20.21	7.11	5.86
2	0.754	0	4.8295	−1.5037	2.4103	24.32	5.49	10.32
2	−0.754	0	4.9977	−2.7165	1.5303	24.99	1.85	8.56
2.389	0	0	5.2527	−2.1890	2.1438	26.01	3.43	9.79
−2.389	0	0	1.0873	−1.2204	0.0132	9.35	6.34	5.53
−2	0.754	0	1.3423	−0.6929	0.6267	10.37	7.92	6.75
−2	−0.754	0	1.5105	−1.9057	−0.2533	11.04	4.28	4.99
2	0	0.528	4.6619	−2.4048	2.3283	23.65	2.79	10.16
2	0	−0.528	5.1653	−1.8154	1.6123	25.66	4.55	8.73
−2	0	0.528	1.1747	−1.5940	0.5447	9.70	5.22	6.59

DISCUSSION AND CONCLUSIONS

It has been found that a selected response (median lethal time) to sodium pentachlorophenate varies with respect to the various levels of quantitative circumstances impressed simultaneously on the test animals. Within the restricted region of the experimental design and its environs there has been found a twofold to threefold variation in the magnitude of the response to the same concentration of pentachlorophenate. Within the computed three-factor domain a point of maximum response has been found which is dependent for its expression on particular levels of the several factors impressed on the animals exposed to the pentachlorophenate.

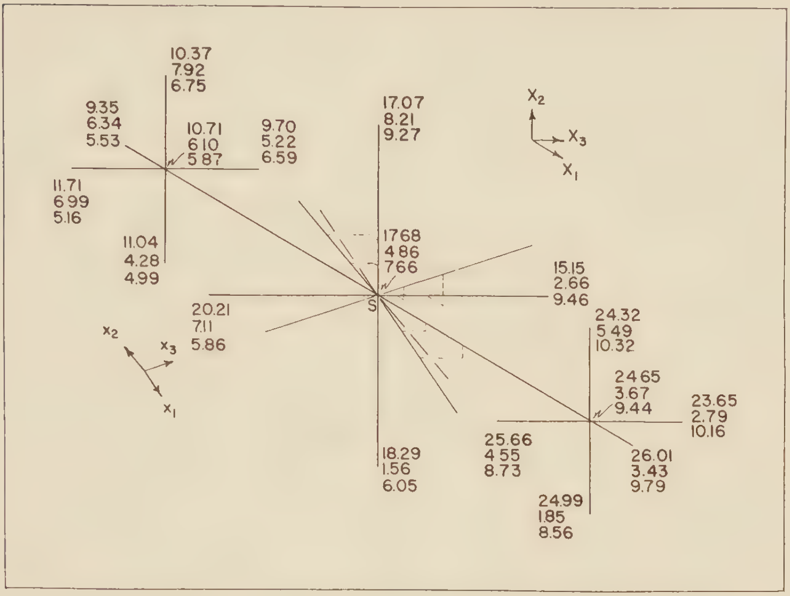
10.37
7.92
6.75
9.35
6.34
5.53
10.71
610
587
9.70
5.22
6.59
17.07
8.21
9.27
X2
X3
X1
11.71
699
5.16
11.04
4.28
4.99
1768
486
766
15.15
2.66
9.46
S
20.21
7.11
5.86
x2
x3
x1
24.32
549
10.32
2465
3.67
9.44
23.65
2.79
10.16
25.66
455
8.73
18.29
1.56
6.05
26.01
3.43
9.79
2499
1.85
8.56

FIG. 2. Loci on the 90% of optimum response envelope of the response ellipsoid in original units. Each triplet of figures refers to salinity, temperature and dissolved oxygen, respectively. The *x*-axes of the experimental factor space have been translocated so that the centre coincides with that of the axes of the response surfaces. Two additional loci on the X_3-axes at $X_3 = \pm 2$, $X_1 = X_2 = 0$ are shown along with that at the centre, *S*.

The main findings of this enquiry may be summarized as follows. The response of the test fish to 3 mg/l of sodium pentachlorophenate over various levels of salinity, temperature and dissolved oxygen was found to be maximal in a region having at its computed centre a locus equivalent to 17.68‰ S, 4.86°C and 7.66 mg/l of dissolved oxygen. On the 90% of optimum response envelope of the ellipsoid with centre at the optimum, the 3 variables were computed to vary between approximately 9 to 26‰ S, 1 to 8°C and 5 to 10 mg/l of dissolved oxygen. On the longest axis of the response ellipsoid, loci on the envelope indicated that within these ranges and in relation to the values at the optimum, higher salinities were coupled with lower temperatures and higher dissolved oxygen levels and lower salinities were coupled with higher temperatures and lower dissolved oxygen levels. On the remaining axes of the response ellipsoid relatively minor changes in salinity with reference to that at the optimum were coupled with relatively larger increases or decreases in temperature and dissolved oxygen level. The nature of these relationships is indicated by the signs of the regression coefficients in the interaction terms of the second-order polynomial relating response to the levels of the three environmental variables. The magnitude of these relationships may be evaluated more completely by inspection of the axes of the response surfaces and boundary loci of Fig. 2.

For the species used in this study it is evident that changes in the nature or levels of other factors associated with the testing of toxic materials may have considerable influence on the resulting response. The standardization of conditions relating to the nature of waters used in particular test situations has been discussed by Doudoroff *et al.* (1951). To obtain estimates of comparative toxicity, in the pharmacological sense, standard testing conditions are essential. In the environmental situation, however, variables which may alter the response by virtue of their presence and levels are not subject to constraint. If the presence or magnitude of certain factors in any water supply is suspected to enter into the definition of response, multivariable analysis of the type here employed should provide insight into these multiple relationships.

For concentration–time relationships and estimates derived from them it follows that experimental variation around such estimates may occur through the association of unknown or unconsidered variables, or the constraining of ancillary variables to operate at fixed levels selected for experimental expediency. Further variation may be related to the geographic location in which testing is conducted and the likelihood of naturally occurring differences in local water supplies influencing experimental results. The nature of such variability may be approximated by the series of hypothetical hyperbolae of Fig. 3 in which threshold values for concentration of a toxic substance, x_0, and for response time, y_0, may vary between maximum and minimum values according to the ancillary circumstances associated with testing. Between the limiting curves a and d therefore may lie an infinite series of hyperbolae relating response and concentration in terms of the levels of other variables associated with the test conditions. Any concentration selected from an experimental curve of this type related to a particular response time (e.g. 48-hour median response time), to derived estimates of "safe" concentration levels (e.g. 48-hour median tolerance limit × 0.1), or even to estimates of x_0 are capable therefore of variation related to ancillary circumstances. The use of such singular estimates as general measures of effect are suspect therefore in the wide range of possible practical circumstances to which a singular estimate might be applied. One is lead to the conclusion that the definition of concentration response relationships could be made more meaningful and generally useful if the potential variation in response associated with the action of environmental variables could be considered simultaneously in the development of these relationships.

It is also possible that the interpretation of experimental alterations in water quality could be improved, resulting in an improved judgment of the significance of existing or potential alterations in the natural environment. The fact that a maximum response, such as a potential for maximum viability in the presence of a pollutant, might be obtained with respect to the presence and levels of other factors operating in the domain is of considerable practical interest. The combination of levels of variables providing maximum viability in the presence of a particular insecticide or industrial effluent, for example, may assist in defining times or locations in which treatments or waste discharge is associated with high or low potential stress in fishes inhabiting the waters con-

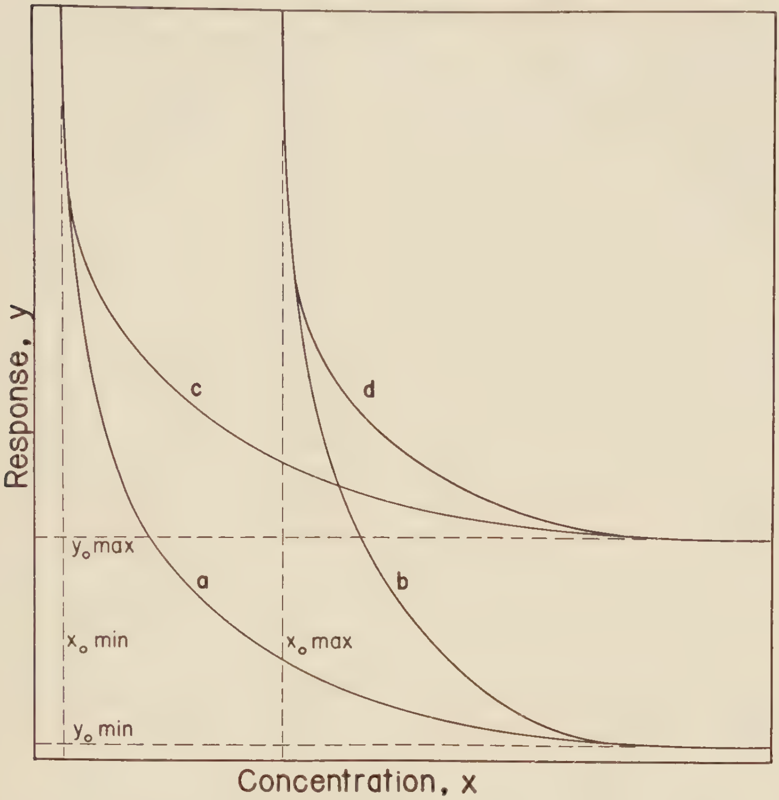

FIG. 3. Hypothetical curves illustrating the manner in which the relationship between concentration of a toxic substance, x, and response, y, might vary under conditions in which ancillary factors associated with the defining relationships are held at various combinations of levels. Curves relating concentration and response could therefore lie anywhere between the limiting curves a and d. Estimates or functions of x_0 would then be capable of variation in absolute value.

sidered. Again, knowledge of the limits of normal variation in the levels of ancillary variables associated with a particular water system, related to the nature of response surfaces for a species subjected to a particular type of pollutant, may define the *background* or experimental levels of ancillary variables which ought to be used in defining limiting values of the concentration–response relationship for the pollutant in question. From another point of view the existence of an optimum in a multivariable response domain implies that there will be envelopes of equal but sub-optimal loci around the domain centre. One might arbitrarily select an envelope at which some pre-selected percentage of maximum viability is retained, in which case there will be a large number of combinations of levels of the variables under consideration which would provide at least the pre-selected percentage of the maximum response possible in terms of a given pollutant. Changes in the levels of factors which yield a net decrease in potential viability, or a movement away from the centre of the response domain will then reflect the presence of an increased stressful situation impressed on fishes inhabiting the affected environment. Extending this approach, water quality might be monitored in terms of a pollutant associated with a water system. Remedial measures could then be taken with respect to pollutant load when alteration in levels of ancillary variables indicated a deterioration in response to a point outside of the boundary provided by an arbitrary envelope, such as that defining combinations of water characteristics for 90% of maximum viability.

Consideration of response surfaces must also be related to species and age or size of fishes. In the case presented, the andromous character of Pacific salmon provides the reason for the consideration of salinity. Preliminary unpublished studies indicate that young coho salmon develop the ability to acclimate to saline water gradually during approximately the 5-month period prior to the time of smolt migration. Examination of response surfaces for coho juveniles subjected to pentachlorophenate indicate that major changes occur in the level of salinity associated with the locus of the optimum over this period (unpublished).

The relationship found between response and the level of temperature at the locus of the optimum is not unexpected in view of the fact that the velocity of a biological response is usually directly related to temperature in poikilothermous animals. Since the temperature of 4.86°C at the optimum is in the lower range of temperature tolerance, the "optimum" temperature would appear to be a compromise between the velocity of lethality for the toxic material and the lower limit of temperature tolerance.

The level of 7.66 mg/l of dissolved oxygen at the locus of the optimum might appear low for Salmonidae as this level is about 69% of saturation. Observations over the test series indicated that discernible differences in activity of test fish were related, at least in part, to dissolved oxygen supply. Activity of the test fish generally was lower in the tests involving low oxygen levels (3–5.5 mg/l). Although there is little direct evidence to support further discussion of this point, examination of the data (see also Fig. 2) indicates that the suggested advantage of high dissolved oxygen levels present at some combinations of temperature and salinity is not present at others. Further tests (unpublished) have suggested the possibility that the response is activity-dependent and that in some cases lower levels of dissolved oxygen may reduce activity and consequently the velocity of the toxic reaction. In judging the significance of these interactions, however, it seems more reasonable to infer that whereas lower dissolved oxygen levels at higher temperatures and lower salinities will still allow 90% of maximum resistance to be expressed, this level of response is only retained at higher salinities and lower temperatures when the dissolved oxygen levels are proportionately higher. It must also be remembered that the discussion of "lower" and "higher" temperatures and dissolved oxygen levels is relative to the ranges computed, namely about 1-8°C and 5–10 mg/l O_2.

Where the experimenter is interested in the response of an animal to the various levels of a complex of variables, the use of extended factorial methods such as those employed should provide certain considerable advantages. It is doubtful if the nature or location of an optimum for multiple factors could be approximated easily by single-factor analyses. In the case examined it is likely that a quasi-optimum would have been selected somewhere on the salinity ridge (compare the values found, for example, for the initial and final determinations of the loci of the region of stationary response). In fact, the single-factor-at-a-time approach to an optimum would have the most reasonable chance for success only where the interaction terms of the polynomial in x are zero; that is, where there is no rotation of axes and those of the design matrix and response surfaces are coplanar.

It may also be argued that where certain constants in the polynomial in x are not significantly different from zero with reference to their standard errors (or where analysis of variance for fitting certain constants indicates a non-significant mean square) then there is justification in deleting these terms from the equation and expressing the response in terms of those remaining. Analysis of variance of the data indicated that the data could be quite adequately represented by the second-degree polynomial less the terms involving x_3. That is, several of the computed regression values are smaller than their standard errors and could be equated to zero. However, since there is no reason to suggest that the values of these constants actually are zero, the best estimates of the constants have been retained (Box, 1956).

The fact that dependence exists between the salinity, temperature and dissolved oxygen variables was indicated in the non-zero values of the b_{12}, b_{13} and b_{23} terms of the polynomial, and illustrated in the non-correspondence of the x-axes and principal axes of the response surfaces (Fig. 2). If the 3 variables were independent, the relationship between axes would be given, for example, by:

$$\begin{bmatrix} x_1 - x_{1S} \\ x_2 - x_{2S} \\ x_3 - x_{3S} \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} . \begin{bmatrix} X_1 \\ X_2 \\ X_3 \end{bmatrix}$$

Hence the levels of temperature and dissolved oxygen coupled with the salinity estimate at the locus 26.01‰ S, 3.43°C and 9.79 mg/l O_2 on the 90% of maximum response boundary on X_1 (Fig. 2) would be those found at the centre S (4.86°C, 7.66 mg/l O_2), instead of those computed (3.43°C, 9.79 mg/l O_2), and the salinity value would be 27.27‰ instead of 26.01‰. Although the interaction terms may be of questionable statistical significance, the likelikood of their biological significance is high and the interaction terms are retained as the best estimates available.

Factorial designs, the basis for the design matrix used in this study, are fundamental to the methods employed. If the present study had utilized 2 replicates of a 3^3 factorial (54 trials) instead of the composite design (30 trials) the experimental time period would have been almost doubled. In this instance the age of the test fish was an important consideration as the response was found to change appreciably with age within the factor space investigated. It therefore was appropriate to complete the tests in the smallest practical time period. The composite design provided the reduced time period at a cost of some loss of sensitivity in determining the estimates of the regression terms. Higher order factorials employing more variables may still accomplish the desired result, for example, by the use of fractional designs in which insignificant interaction terms discovered from initial trials are equated to new variables.

A consideration of the errors involved in the analysis of the experimental data is essential in evaluating the significance of the results obtained. A discussion of the theory in this regard may be found by consulting the original papers of Box and associates. The methods employed here were originally outlined by them for the type of problem in which the experimental error could be expected to be small. Hence, if data are fitted to a second-order polynomial with evidence that higher order effects are of no significance, then the regression terms may be estimated with fairly high precision. In this instance the experimental error, although not unduly large, is greater than is theoretically desirable. The magnitude of experimental error as well as the fact that the quadratic effects are computed with half the precision of the interaction effects are reflected in the size of the standard errors of the estimates of the regression terms. Evaluation of the response surfaces by reduction of the polynomial to its canonical form, and estimates of the point or region of stationary response will be dependent to a large extent on the validity of the best estimates of the regression terms employed. For this reason the levels of salinity, temperature and dissolved oxygen computed from the data, although they have been set down as calculated, should be considered only as the best estimates obtained from the data. The sequential addition of the extra experimental points (trials 16–25) also reduces the variance of the estimates as can be seen by comparison of the initial and final computed standard errors of the regression coefficients.

The nature of the response surfaces as determined and their validity in representing the data will be influenced initially by the judgement of the experimenter in defining the experimental factor space in reasonable proximity to the central region of the response configuration. If the initial factor space is at a distance from a region of stationary response and quadratic terms are appreciable in comparison with the main effects, the path of steepest ascent toward the region of near-stationary response may miss the region entirely. The procedures will define the nature of the response surfaces best within the confines of the factor space examined. However, once the region of stationary response has been approximated by trials extending toward it, a further design to examine the factor space in that region will provide better definition of the response surfaces in the central region. Unfortunately, in the present case, by the time trials had indicated the general region of stationary response further examination of this region had been precluded by the time elapsed from the start of the enquiry and the fact that the fish were known to show marked changes in response with increasing age. Redesign of experimental equipment will minimize this problem now that the fact is known that rapid changes in response characteristics may occur. Again, increased knowledge of the experimental animal responses gained from initial studies provides the information upon which more judicious choice of the experimental factor space may be made. Iterative steps toward a region of stationary response may be minimized in this manner in succeeding designs.

It may be argued that the magnitude of experimental error inherent in biological problems of this type raises the question as to whether such methods of analysis should be employed. An analysis of the response surfaces over the whole domain employing levels of each variable extending to the upper and lower limits of the zones of tolerance for each variable would require much larger experiments than have been conducted in this instance. However, rather than to attempt elucidation of the total domain in one design, very useful information on the relative magnitude of effect and multifactor dependence would be available from examination of specific regions, depending on the questions posed by the initial enquiry. One region of particular interest would most certainly be that of the domain centre or region of stationary response.

The alternative to examining responses to a complex of interacting environmental factors is that of isolating factors for individual study. Such individual relationships may be well defined experimentally, and have contributed to the cataloguing of what have become known as physiological parameters. However, if one is to examine the manner in which the response of an animal to a variable may be altered by the simultaneous action and interaction of other variables in the environmental complex, the extension of techniques to allow evaluation of multifactor dependence is an inescapable requirement (e.g. Fisher, 1949, sect. 37). In this instance the data have indicated that the response to sodium pentachlorophenate is neither linearly related to levels of salinity, temperature or dissolved oxygen impressed simultaneously on the test animals, nor do these factors operate independently in altering the response of the animal to the pollutant.

In view of the increasing demands of multiple water usage and the alterations in water quality which frequently attend multiple use, the necessity for judging the significance of water quality alterations on aquatic animals is increasingly evident. By accepting the fact that the environment is complex and adopting methods of analysis which allow some comprehension of the operation of the complex, it is concluded that a more meaningful evaluation of the effects of water quality alteration on associated fishes may be achieved.

ACKNOWLEDGMENTS

The experimental work upon which this study is based is part of a larger programme in which the laboratory assistance of Mr F. P. J. Velsen is gratefully acknowledged. Discussions with and criticisms of many others have been much appreciated, among them Dr S. W. Nash, Department of Mathematics, University of British Columbia, Mr W. P. Wickett, and Drs J. R. Brett, N. P. Fofonoff, J. D. H. Strickland and T. R. Parsons of the Nanaimo Station. Grateful thanks are extended to Mr W. Caulfield and Mr H. Neate for their considerable assistance in the collection of young salmon used in the tests. The author is also indebted to Dr Charlotte Froese, Computing Centre, University of British Columbia, who programmed the design employed and analyses for computer operation. Dr D. B. DeLury, Department of Mathematics, University of Toronto, read the preliminary manuscript. His helpful criticisms and advice are gratefully recorded.

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APPENDICES

Although it is not essential to the development of the arguments upon whic this paper is based, nervertheless, some indication of the methods of analysi employed will be outlined briefly as appendices. The sections below are referre to in the text.

A. Since in the orthogonal composite factorial design employed, the mean an quadratic effects are confused with one another, the sums of squares in analysi of variance are not additive. Estimation of sums of squares is simplified b orthogonalizing the matrix of independent variables. The independent variable in Table I with n trials for k variables form an $n \times k$ matrix **D** designated th design matrix. The n values of the vector **Y** constitute the observed response within this experimental design. The second order polynomial to which th data are fitted contains L = 10 terms $x_0, x_1, \ldots, x_1^2, \ldots, x_1x_3, \ldots, x_2x_3$, an these, the powers and products of the co-ordinates of the experimental points ar the independent variables. The matrix of independent variables **X** consist therefore of n values of L functions of the co-ordinates. In **X**:

$$\begin{aligned} \Sigma x_1/n &= \Sigma x_2/n &&= \Sigma x_3/n &&= 0 \\ \Sigma x_1^2/n &= \Sigma x_2^2/n &&= \Sigma x_3^2/n &&= 0.73016 \\ \Sigma x_1x_2/n &= \Sigma x_1x_3/n &&= \Sigma x_2x_3/n &&= 0 \end{aligned}$$

for the $2^k + 2k + 1$ point design employed. To achieve complete orthogonality in **X** the following adjustment is made; in the polynomial:

$$z = \beta_0 x_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_{11} x_1^2 + \beta_{22} x_2^2 + \beta_{33} x_3^2 + \beta_{12} x_1 x_2 + \beta_{13} x_1 x_3 + \beta_{23} x_2 x_3$$

the mean of the z's

$$z_0 = \beta_0 + \beta_{11}(0.73016) + \beta_{22}(0.73016) + \beta_{33}(0.73016)$$

Subtracting the latter from the former

$$\begin{aligned} z = z_0 x_0 &+ \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_{11}(x_1^2 - 0.73016) + \beta_{22}(x_2^2 - 0.73016) \\ &+ \beta_{33}(x_3^2 - 0.73016) + \beta_{12} x_1 x_2 + \beta_{13} x_1 x_3 + \beta_{23} x_2 x_3 \end{aligned}$$

This adjustment to the n values of the co-ordinates of the experimental points for the quadratic terms provides complete orthogonality, since the sum of products for any two columns in the adjusted matrix **X** is zero. The effects may be estimated directly, for with the elements of the appropriate independent variable,

$$b = \Sigma xy/\Sigma x^2$$

and the sum of squares [S of S] for b in the analysis of variance is:

$$\text{S of S} = (\Sigma xy)^2/\Sigma x^2$$

The treatment sum of squares may accordingly be partitioned directly into sums of squares for each of the 9 coefficients, apart from z_0, and the remainder (Treatment S of S − Regression S of S for fitting $\beta_1 \ldots \beta_{23}$) yields the S of S for deviations from regression (Box and Wilson, 1951: Box, 1956).

B. The regression constants may be obtained as indicated in Appendix A. Generally, it was found more convenient to derive **B**, the vector of *b*'s from

$$\mathbf{B} = \mathbf{TY}$$

where **T**, the transforming matrix, is $(\mathbf{X}'\mathbf{X})^{-1}\mathbf{X}'$. Hence, where:

$$X = \begin{array}{r|cccccccccc|}
 & x_0 & x_1 & x_2 & x_3 & x_1^2 & x_2^2 & x_3^2 & x_1x_2 & x_1x_3 & x_2x_3 \\
1 & 1 & -1 & -1 & -1 & 1 & 1 & 1 & 1 & 1 & 1 \\
2 & 1 & -1 & -1 & 1 & 1 & 1 & 1 & 1 & -1 & -1 \\
3 & 1 & -1 & 1 & -1 & 1 & 1 & 1 & -1 & 1 & -1 \\
4 & 1 & -1 & 1 & 1 & 1 & 1 & 1 & -1 & -1 & 1 \\
5 & 1 & 1 & -1 & -1 & 1 & 1 & 1 & -1 & -1 & 1 \\
6 & 1 & 1 & -1 & 1 & 1 & 1 & 1 & -1 & 1 & -1 \\
7 & 1 & 1 & 1 & -1 & 1 & 1 & 1 & 1 & -1 & -1 \\
8 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\
9 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
10 & 1 & -1.215 & 0 & 0 & 1.476225 & 0 & 0 & 0 & 0 & 0 \\
11 & 1 & 1.215 & 0 & 0 & 1.476225 & 0 & 0 & 0 & 0 & 0 \\
12 & 1 & 0 & -1.215 & 0 & 0 & 1.476225 & 0 & 0 & 0 & 0 \\
13 & 1 & 0 & 1.215 & 0 & 0 & 1.476225 & 0 & 0 & 0 & 0 \\
14 & 1 & 0 & 0 & -1.215 & 0 & 0 & 1.476225 & 0 & 0 & 0 \\
15 & 1 & 0 & 0 & 1.215 & 0 & 0 & 1.476225 & 0 & 0 & 0
\end{array}$$

$$X'X = \begin{array}{r|cccccccccc|}
 & x_0 & x_1 & x_2 & x_3 & x_1^2 & x_2^2 & x_3^2 & x_1x_2 & x_1x_3 & x_2x_3 \\
x_0 & 15 & 0 & 0 & 0 & 10.95245 & 10.95245 & 10.95245 & 0 & 0 & 0 \\
x_1 & 0 & 10.95245 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
x_2 & 0 & 0 & 10.95245 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
x_3 & 0 & 0 & 0 & 10.95245 & 0 & 0 & 0 & 0 & 0 & 0 \\
x_1^2 & 10.95245 & 0 & 0 & 0 & 12.35848 & 8.0 & 8.0 & 0 & 0 & 0 \\
x_2^2 & 10.95245 & 0 & 0 & 0 & 8.0 & 12.35848 & 8.0 & 0 & 0 & 0 \\
x_3^2 & 10.95245 & 0 & 0 & 0 & 8.0 & 8.0 & 12.35848 & 0 & 0 & 0 \\
x_1x_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 8.0 & 0 & 0 \\
x_1x_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 8.0 & 0 \\
x_2x_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 8.0
\end{array}$$

$$
(X'X)^{-1} = \begin{array}{c|cccccccccc}
 & x_0 & x_1 & x_2 & x_3 & x_1^2 & x_2^2 & x_3^2 & x_1x_2 & x_1x_3 & x_2x_3 \\
\hline
x_0 & .432899 & 0 & 0 & 0 & -.167192 & -.167192 & -.167192 & 0 & 0 & 0 \\
x_1 & 0 & .091304 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
x_2 & 0 & 0 & .091304 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
x_3 & 0 & 0 & 0 & .091304 & 0 & 0 & 0 & 0 & 0 & 0 \\
x_1^2 & -.167192 & 0 & 0 & 0 & .229285 & -.000153 & -.000153 & 0 & 0 & 0 \\
x_2^2 & -.167192 & 0 & 0 & 0 & -.000153 & .229285 & -.000153 & 0 & 0 & 0 \\
x_3^2 & -.167192 & 0 & 0 & 0 & -.000153 & -.000153 & .229285 & 0 & 0 & 0 \\
x_1x_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & .1250 & 0 & 0 \\
x_1x_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & .1250 & 0 \\
x_2x_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & .1250
\end{array}
$$

$$
T' = \begin{array}{c|cccccccccc}
 & b_0 & b_1 & b_2 & b_3 & b_{11} & b_{22} & b_{33} & b_{12} & b_{13} & b_{23} \\
\hline
1 & -0.0687 & -0.0913 & -0.0913 & -0.0913 & 0.0618 & 0.0618 & 0.0618 & 0.1250 & 0.1250 & 0.1250 \\
2 & -0.0687 & -0.0913 & -0.0913 & 0.0913 & 0.0618 & 0.0618 & 0.0618 & 0.1250 & -0.1250 & -0.1250 \\
3 & -0.0687 & -0.0913 & 0.0913 & -0.0913 & 0.0618 & 0.0618 & 0.0618 & -0.1250 & 0.1250 & -0.1250 \\
4 & -0.0687 & -0.0913 & 0.0913 & 0.0913 & 0.0618 & 0.0618 & 0.0618 & -0.1250 & -0.1250 & 0.1250 \\
5 & -0.0687 & 0.0913 & -0.0913 & -0.0913 & 0.0618 & 0.0618 & 0.0618 & -0.1250 & -0.1250 & 0.1250 \\
6 & -0.0687 & 0.0913 & -0.0913 & 0.0913 & 0.0618 & 0.0618 & 0.0618 & -0.1250 & 0.1250 & -0.1250 \\
7 & -0.0687 & 0.0913 & 0.0913 & -0.0913 & 0.0618 & 0.0618 & 0.0618 & 0.1250 & -0.1250 & -0.1250 \\
8 & -0.0687 & 0.0913 & 0.0913 & 0.0913 & 0.0618 & 0.0618 & 0.0618 & 0.1250 & 0.1250 & 0.1250 \\
9 & 0.4329 & 0 & 0 & 0 & -0.1672 & -0.1672 & -0.1672 & 0 & 0 & 0 \\
10 & 0.1861 & -0.1109 & 0 & 0 & 0.1713 & -0.1674 & -0.1674 & 0 & 0 & 0 \\
11 & 0.1861 & 0.1109 & 0 & 0 & 0.1713 & -0.1674 & -0.1674 & 0 & 0 & 0 \\
12 & 0.1861 & 0 & -0.1109 & 0 & -0.1674 & 0.1713 & -0.1674 & 0 & 0 & 0 \\
13 & 0.1861 & 0 & 0.1109 & 0 & -0.1674 & 0.1713 & -0.1674 & 0 & 0 & 0 \\
14 & 0.1861 & 0 & 0 & -0.1109 & -0.1674 & -0.1674 & 0.1713 & 0 & 0 & 0 \\
15 & 0.1861 & 0 & 0 & 0.1109 & -0.1674 & -0.1674 & 0.1713 & 0 & 0 & 0
\end{array}
$$

The sum of products of the elements of **Y** with the columns of **T′** provide the estimates b_0, b_1, b_2, . . ., b_{23}.

Standard errors of the estimates are now conveniently obtained by multi- plication of the appropriate diagonal elements of $(\mathbf{X}'\mathbf{X})^{-1}$ by s^2, computed initiall in this case as 62.84, providing the variances of the b's and hence their standard errors.

Inversion of large matrices such as $(\mathbf{X}'\mathbf{X})^{-1}$ is most effectively undertake by initially partitioning into sub-matrices (e.g. Turnbull and Aitken, 1961 followed by computational devices such as that of Box (1956), or standar algebraic schemes such as that in which the inverse of the matrix is found by division of the adjoint of the matrix by its determinant (e.g. Weiss, 1949).

C. Since:

$$\frac{\partial Y}{\partial x_1} = b_1 + 2b_{11}x_1 + b_{12}x_2 + b_{13}x_3 = 0$$

$$\frac{\partial Y}{\partial x_2} = b_2 + b_{12}x_1 + 2b_{22}x_2 + b_{23}x_3 = 0$$

$$\frac{\partial Y}{\partial x_3} = b_3 + b_{13}x_1 + b_{23}x_2 + 2b_{33}x_3 = 0$$

Therefore:

$$b_{11}x_1 + \tfrac{1}{2}b_{12}x_2 + \tfrac{1}{2}b_{13}x_3 = -\tfrac{1}{2}b_1$$

$$\tfrac{1}{2}b_{12}x_1 + b_{22}x_2 + \tfrac{1}{2}b_{23}x_3 = -\tfrac{1}{2}b_2$$

$$\tfrac{1}{2}b_{13}x_1 + \tfrac{1}{2}b_{23}x_2 + b_{33}x_3 = -\tfrac{1}{2}b_3$$

and:

$$5.458 - 1.250 + 1.250 = -4.524$$

$$-1.250 - 1.993 + 0.125 = 5.130$$

$$1.250 + 0.125 - 2.671 = 0.004$$

Large systems of such equations may be solved by various methods (Box, 1956; Fox, 1950; Smith, 1954). For up to 3 variables solution is achieved very simply by substitution of the column on the left–hand side containing the unknown sought by the elements of the column on the right–hand side and division of the resulting determinant by the determinant of the original matrix of quadratic and interaction terms (Δ). For example where:

$$\mathbf{B} = \begin{bmatrix} b_{11} & \tfrac{1}{2}b_{12} & \tfrac{1}{2}b_{13} \\ \tfrac{1}{2}b_{12} & b_{22} & \tfrac{1}{2}b_{23} \\ \tfrac{1}{2}b_{13} & \tfrac{1}{2}b_{23} & b_{33} \end{bmatrix} \qquad x_{1S} = \begin{vmatrix} -4.524 & -1.250 & 1.250 \\ 5.130 & -1.993 & 0.125 \\ 0.004 & 0.125 & -2.671 \end{vmatrix} \Big/ \Delta$$

D. Solution of the "characteristic equation" for its roots may be achieved by various methods of which the following has been found most convenient.

For various arbitrary values of λ (e.g. 0, 1, 2, 3, ...) values of f(λ) are calculated. A plot of λ against f(λ) will provide three approximations (the roots all being real) to the value of λ at which $f(\lambda) = 0$.

One estimate of λ is selected and its real value is approximated with a high degree of accuracy by "Newton's method" (Lanczos, 1956). Thus if a good approximation of one root $\lambda = \lambda_0$ has been obtained, an improved estimate may be calculated where

$$\lambda_1 = \lambda_0 + h_0$$

$$\frac{1}{h_0} = -\frac{f'(\lambda_0)}{f(\lambda_0)} + \tfrac{1}{2}\frac{f''(\lambda_0)}{f'(\lambda_0)}$$

f, f′, and f″ being the characteristic equation and its first and second derivatives respectively. If necessary, a second cycle may be calculated where

$$\lambda_2 = \lambda_1 + h_1$$

$$\frac{1}{h_1} = -\frac{f'(\lambda_1)}{f(\lambda_1)} + \tfrac{1}{2}\frac{f''(\lambda_1)}{f'(\lambda_1)}$$

If λ_0 has been a reasonably close approximation, iteration toward $f(\lambda) = 0$ will be rapid. Having obtained one of the roots of the cubic, "synthetic division" of the characteristic equation by the computed root provides a quadratic in the remaining two roots whose solution is straightforward.

E. The addition of extra observations does not require a complete recalculation of $(\mathbf{X}'\mathbf{X})^{-1}$. In the notation of Box and Wilson (1951) adjustments, attributed to Plackett, may be made to previous estimates with a minimum of recalculation.

If to N_1 initial observations N_2 extra observations $\mathbf{Z}$ are added corresponding to a set of points whose co-ordinates are given by $\mathbf{D}_2$ for which the matrix of independent variables is $\mathbf{W}$, and $\mathbf{S}$ the residual sum of squares has been calculated, then

$$\begin{aligned} (\mathbf{X}'\mathbf{X})^{-1} &= (\mathbf{X}'\mathbf{X})^{-1} - \mathbf{JGJ} \\ \mathbf{B}_0' &= \mathbf{B}' + \Delta'\mathbf{GJ} \\ \mathbf{S}_0 &= \mathbf{S} + \Delta'\mathbf{G}\Delta \end{aligned}$$

where

$$\mathbf{J} = \mathbf{W}(\mathbf{X}'\mathbf{X})^{-1}, \quad \mathbf{G} = (\mathbf{J} + \mathbf{R})^{-1}, \quad \mathbf{R} = \mathbf{W}(\mathbf{X}'\mathbf{X})^{-1}\mathbf{W}', \quad \Delta = \mathbf{Z} - \mathbf{WB}$$

F. For the determinant

$$(B - \lambda I) = \begin{vmatrix} b_{11}-\lambda & \frac{1}{2}b_{12} & \frac{1}{2}b_{13} \\ \frac{1}{2}b_{12} & b_{22}-\lambda & \frac{1}{2}b_{23} \\ \frac{1}{2}b_{13} & \frac{1}{2}b_{23} & b_{33}-\lambda \end{vmatrix} = 0$$

matrices of cofactors B are obtained where $\lambda = \lambda_{11}$, λ_{22} and λ_{33} respectively. From each matrix of cofactors is obtained a row vector proportional to the cofactors of the elements in each row of the determinant (Hildebrand, 1952). To preserve orthogonality each vector is divided by the square root of the sum of squares of its elements, in which case the sum of squares in any row or column of the resulting eigenvectors will be unity while the sum of products in different rows will be zero. Hence, for the final computed value of $\lambda_{11} = -1.47759$, the cofactors B of the determinant $|\mathbf{B} - \lambda\mathbf{I}| = 0$ are

$$\begin{vmatrix} B_{11} & B_{12} & B_{13} \\ B_{21} & B_{22} & B_{23} \\ B_{31} & B_{32} & B_{33} \end{vmatrix} = \begin{vmatrix} 7.46929 & -1.73678 & 3.82026 \\ -1.73678 & 0.40384 & -0.88829 \\ 3.82026 & -0.88829 & 1.95391 \end{vmatrix}$$

and: $m_1 = [B_{11/d}, B_{12/d}, B_{13/d}] = [m_{11}, m_{12}, m_{13}]$
$= [0.87182 \ -0.20271 \ 0.44590]$

where: $d = \sqrt{\Sigma(B_{11}^2 + B_{12}^2 + B_{13}^2)}$

Similarly for $\lambda_{22} = -4.44030$:

$$m_2 = [m_{21}, m_{22}, m_{23}] = [-0.11147 \quad 0.80433 \quad 0.58362]$$

and for $\lambda_{33} = -4.79450$

$$m_3 = [m_{31}, m_{32}, m_{33}] = [0.47696 \quad 0.55856 \quad -0.67860]$$

Associating the λ roots with the elements in the vector implying least rotation and multiplying the respective vectors by -1 where these values are negative:

$$\begin{array}{c} \begin{array}{ccc} \lambda_{11} & \lambda_{22} & \lambda_{33} \end{array} \\ \begin{bmatrix} 0.87182 & -0.11147 & -0.47696 \\ -0.20271 & 0.80433 & -0.55856 \\ 0.44590 & 0.58362 & 0.67860 \end{bmatrix} \end{array} = \mathbf{M}$$

Thus, a check on the calculations may be made by premultiplication of the matrix of quadratic and interaction terms $\mathbf{B}$ by the transpose of $\mathbf{M}$, and postmultiplication by $\mathbf{M}$, yielding the matrix of eigenvalues $\mathbf{\Lambda}$ in the principal diagonal, all terms off the principal diagonal being zero. Hence, since: $\mathbf{BM} = \mathbf{M\Lambda}$ and $\mathbf{M'M} = \mathbf{I}$:

$$\begin{aligned} \mathbf{M'BM} &= \mathbf{M'M\Lambda} \\ &= \mathbf{\Lambda}. \end{aligned}$$

Seasonal Movements of the Winter Flounder, *Pseudopleuronectes americanus* (Walbaum), on the Atlantic Coast[1,2]

By F. D. McCracken

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

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[1] Received for publication August 17, 1962.

[2] Based on a thesis accepted by the School of Graduate Studies, University of Toronto, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

J. Fish. Res. Bd. Canada, 20(2), 1963.
Printed in Canada.

ABSTRACT

Winter flounders occur from Labrador to Georgia and yield large catches off southern New England. This paper relates their distribution and seasonal movements to environmental factors.

In spring immature and mature flounders are alongshore with spawning fish concentrated in shallow water. During "summer", winter flounders leave the shore zone in areas where water temperatures rise above about 15°C but not where bottom temperatures do not reach this level. This movement toward cooler water does not continue into depths at which temperature is below about 12°C. Flounders return to the shore zone in fall after temperature decreases below 15°C. These temperatures are well below the upper incipient lethal for flounders of about 26°C.

Flounders remaining alongshore in summer are distributed in depth according to size and maturity. Small, immature fish are in the shallowest water, the region of highest light intensity, immatures of medium size deeper, and mature fish in both regions. Under experimental conditions immature fish of medium size moved into shade at lower light intensities than either small immatures or large matures.

North of Cape Cod flounders move deeper in "winter" as the shallow water becomes colder than the deeper. To the south spawning condition is reached earlier and mature flounders remain in shallow water during the cold-water period.

Off southern New England a large, sustained fishery denotes a large population of flounders. In the Bay of Fundy and off the coast of Nova Scotia winter flounders are restricted to a narrow depth zone, and good exploratory catches there probably do not indicate large populations. In the broader shallow zones of the southern Gulf of St. Lawrence similar catches suggest a larger population. Exploitation will depend on increased efforts by small otter trawlers or possible development of marine sport fishing.

INTRODUCTION

The winter flounder, *Pseudopleuronectes americanus* (Walbaum), is found along the Atlantic coast of North America from Labrador to Georgia.

Off the New England States and New York, landings of this species have reached 25 million lb annually in the late 1940's, but more recently have been around 15 million lb. A number of authors (Bigelow and Schroeder, 1953; Lobell, 1939; Perlmutter, 1940, 1947) agree that in this region the winter flounder makes more or less regular migrations. They are found on or near the bottom in deeper offshore waters in the summer and in the winter are found in the shallows where they spawn.

Off the Canadian coast the winter flounder was of little commercial value when this study was begun in 1947. Small amounts were used locally for lobster bait. It was known that winter flounders were common in various localities along the coasts of New Brunswick, Nova Scotia and Prince Edward Island, and it seemed possible that a fishery for this species might be developed in Canadian waters. To help assess this potentiality an investigation of seasonal distribution of winter flounders in specific Canadian regions was carried out by exploratory fishing. Observations on sexual maturity, length and age were related to depth distribution. A relation between its depth distribution and water temperature has been developed by comparing observations under widely different temperature conditions in Canadian and United States waters. Tolerance limits for high temperature and reduced salinity were defined in the laboratory, and observations were made on the behaviour of different sizes of winter flounders in relation to light intensity.

SEASONAL DEPTH DISTRIBUTION BY AREA

The occurrence of winter flounders in relatively localized areas over a wide north–south range (Fig. 1) provided opportunity to consider their seasonal distribution and movements relative to area and to various factors of the environment. Since the winter flounder is a bottom-living fish, changes in depth generally correspond with changes in distance from shore.

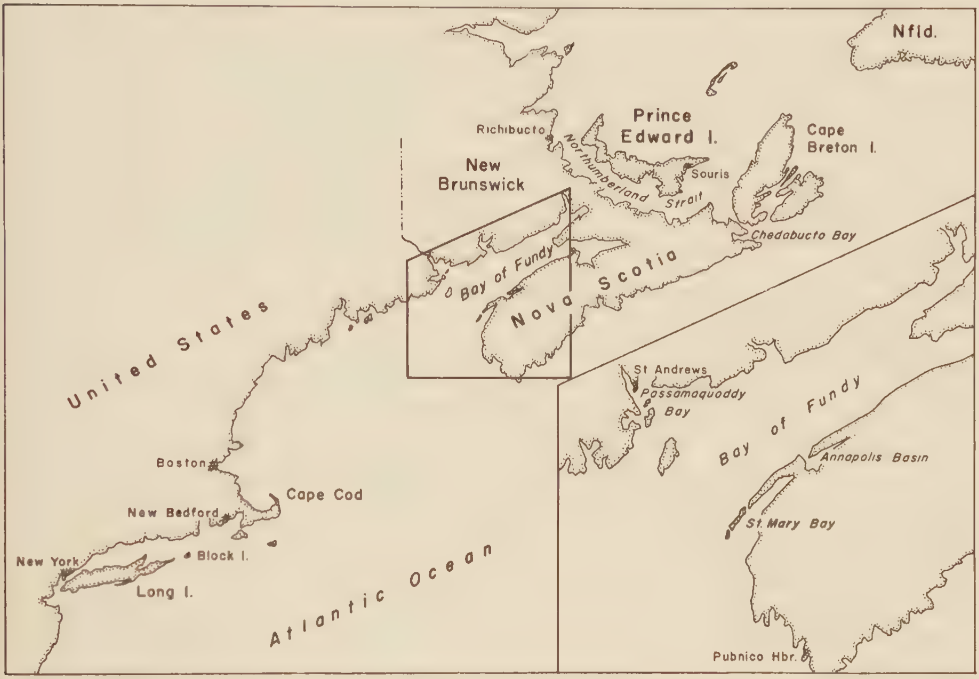
Nfld.
Prince Edward I.
Richibucto
Northumberland Strait
Souris
Cape Breton I.
New Brunswick
Chedabucto Bay
Bay of Fundy
Nova Scotia
United States
Boston
Cape Cod
New Bedford
Block I.
New York
Long I.
Atlantic Ocean
St Andrews
Passamaquoddy Bay
Bay of Fundy
Annapolis Basin
St. Mary Bay
Pubnico Hbr.

FIG. 1. Location of areas in which winter flounder distribution is considered and Canadian regions where exploratory fishing was carried out during this study.

Exploratory fishing in the Canadian region during this study was mainly with beam trawl, flounder drag, shrimp trawl and Danish seine. The beam trawl with its more constant mouth gape was used for most of the repetitive sampling in Passamaquoddy Bay, Pubnico Harbour and off Souris. Set seines which were occasionally used, trapped flounders on the beach within the intertidal zone by blocking their escape from the drying flats. Time of sampling and gear used in each of the Canadian localities are presented in Table I.

Usually all flounders caught were measured to the nearest centimetre from the tip of the snout to the end of the caudal fin. Occasionally, when catches were large, a random sample of the catch was taken for measuring. The sample was taken by spreading the fish on deck, mixing them up, dividing the catch approximately in half, and repeating the process until a sample of suitable size was obtained.

TABLE I. Localities sampled and methods used.

Locality (Fig. 1)	Date	Details of method
St. Mary Bay, N.S.	1948–1952 fishing season Apr.–Nov.	Records of commercial fishery—kept by dragger operators showing catch by species, numbers of drags, hours dragged, place, depth and date; checked by interviews and trips on draggers.
	1949 and 1950	Tagging—see page 564 for numbers and methods.
Pubnico Harbour, N.S.	1948—May, June, July and October	Beam trawl—sampled by means of 15-minute drags with a 12-foot (3.6 m) beam trawl, from the shallow to the deepest water in this harbour.
Outer coast of Nova Scotia	1947–1951 various times of year	Various gears—shrimp trawl (38-ft (11.5 m) headline), flounder drags (40-, 50- and 60-ft (12-, 15- and 18-m) headlines) and a Danish seine.
Northumberland Strait	1949—July and September	Beam trawl—sampled by means of 15-minute drags off Souris, P.E.I., with a 12-foot beam trawl.
	1951—August, October and November	Flounder drag—explored in eastern Northumberland Strait by means of 30-minute tows with a flounder drag (50-ft headline).
Passamaquoddy Bay, N.B.	May 1947–March 1950	Beam trawl—15-minute drags at intervals throughout this period at the sampling stations shown in Fig. 3; occasional drags within the intertidal zone; set seine—at intervals within intertidal zone (see text for description of method); flounder drag—occasional samples with a drag (40-ft headline).

Gonads were exposed by opening the body cavity, the sex was noted and the state of maturity recorded from field examinations for all fish from Passamaquoddy Bay and most fish from other localities.

Otoliths were removed from all fish taken in Passamaquoddy Bay from May 1947 to April 1948 and preserved in a mixture of glycerin and water. Samples of otoliths were taken from other localities. Otoliths were read under reflected light without sectioning.

PASSAMAQUODDY BAY

Physical features of Passamaquoddy Bay have been recorded in detail by Chevrier and Trites (1960). References to tidal amplitudes, temperatures and salinities will be made as required. Although no continuing commercial fishery for winter flounders occurs within this Bay, a sampling program started in May 1947 and continued at intervals until March 1950 permits a detailed account of winter flounder distribution there. Sampling locations are shown in Fig. 2.

SEASONAL DISTRIBUTION BY MATURITY AND AGE. Comparisons of catch per drag by a beam trawl (Fig. 3 and 4) show differences in distribution by age and maturity, particularly during summer months, in Passamaquoddy Bay. Fish-of-the-year, 1947 year-class, were absent from trawl catches until November although caught in the shallow shore seine hauls by July. From May to September immature fish of all ages were concentrated at depths less than 10 fathoms (18 m). Those of the 1946 year-class, age I in 1947, were shallowest, at depths less than 5 fathoms (9 m), until September, when they tended to move into the 6- to 10-fathom zone (11–18 m). Older immatures were most concentrated between 6 to 10 fathoms throughout this period. By November age I and II immature fish were most numerous in the 6- to 10-fathom zone, while age III and older were deeper.

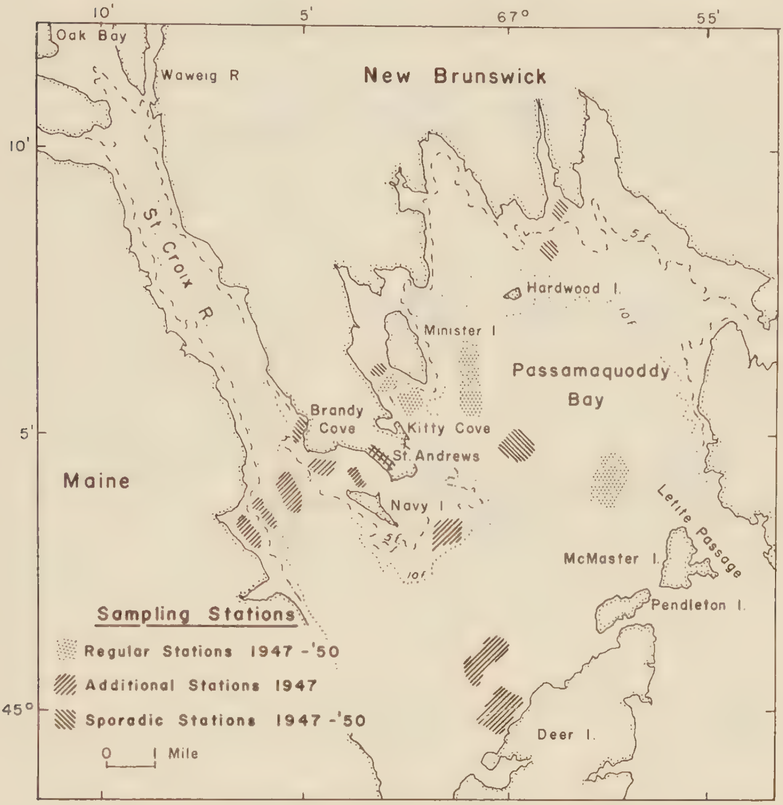
10'
5'
67°
55'
10'
5'
45°
Oak Bay
Waweig R
New Brunswick
St. Croix R
Hardwood I.
Minister I
Passamaquoddy Bay
Brandy Cove
Kitty Cove
St. Andrews
Maine
Navy I
Letite Passage
McMaster I.
Pendleton I.
Deer I.
Sampling Stations
Regular Stations 1947 -'50
Additional Stations 1947
Sporadic Stations 1947 -'50
0 1 Mile
5f
10f

FIG. 2. Location of sampling stations in Passamaquoddy Bay.

Winter catches of immature fish (January and March) were negligible in depths less than 10 fathoms. Catches from deeper than 10 fathoms were greater but much below the summer shallow-water catch level. By April catch per drag had increased markedly in the deeper waters below 10 fathoms.

At spawning time, in May, mature fish of all ages were concentrated in the shallows, between 0 and 5 fathoms (0–9 m), and throughout the summer catches of mature fish of all ages remained greatest there. However, by June, some mature fish were dispersed into the deeper water of the Bay, and distribution remained stable throughout the remainder of the summer. By November abundance of mature fish in shallow water was much reduced with greatest catches occurring between 6 and 10 fathoms.

In winter, January–March, mature flounders were not taken in the shallow water and catches were much reduced in the deeper water of the Bay. By April greatly increased catch per effort marked a distribution of mature fish throughout the depth range of the Bay.

COMPARISON OF DISTRIBUTION FOR DIFFERENT YEARS. In the years 1947–50 the seasonal changes in distribution of winter flounders in Passamaquoddy Bay

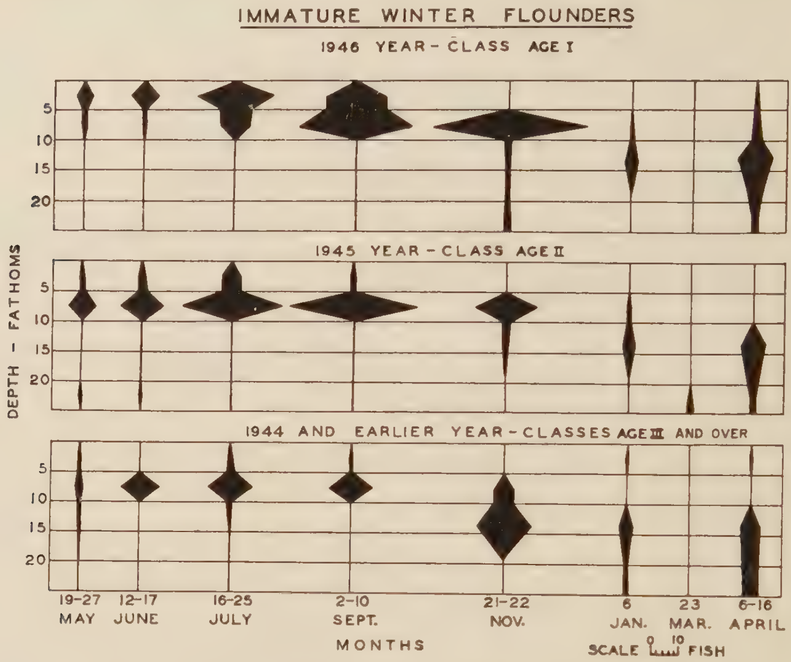

FIG. 3. Catch of immature winter flounders per 15-minute drag in Passamaquoddy Bay, by depth, age and month, during the period May 1947 to April 1948.

follow the same general pattern in each year (Fig. 5 and 6). By fall (November and December) both small and large fish had begun to move offshore to deeper water and were most numerous in intermediate depths, 6 to 20 fathoms (11–37 m).

Catches of both large and small fish were much reduced by January at all depths, with the exception of January 1949 when catches of small fish were high at intermediate depths. Catch per tow was decreased further in February and March for all years, with maximum catches at this season taken generally in deeper water. Catch per effort within the Bay was higher in the winter of 1949 than in 1948 and 1950, but still much below summer and fall levels. Lowest catches occurred in 1948, the coldest year.

Although spring sampling was less complete than that in the fall and winter, the results in both 1948 and 1949 show much increased catch per effort by April–May (Fig. 5 and 6). Both small and large fish moved back into shallow water. They also extended throughout all depths of the Bay. Sampling in 1948 showed that availability had increased by mid April. In 1949 availability was only slightly increased in early April, but had increased markedly by mid May. Supplementary sampling with a flounder drag in mid April produced numerous flounders with catch per effort about twice as great in deep water as in shallow.

Apparently, increased availability of winter flounders in Passamaquoddy Bay occurs in early April as fish move back into shallower waters of the Bay.

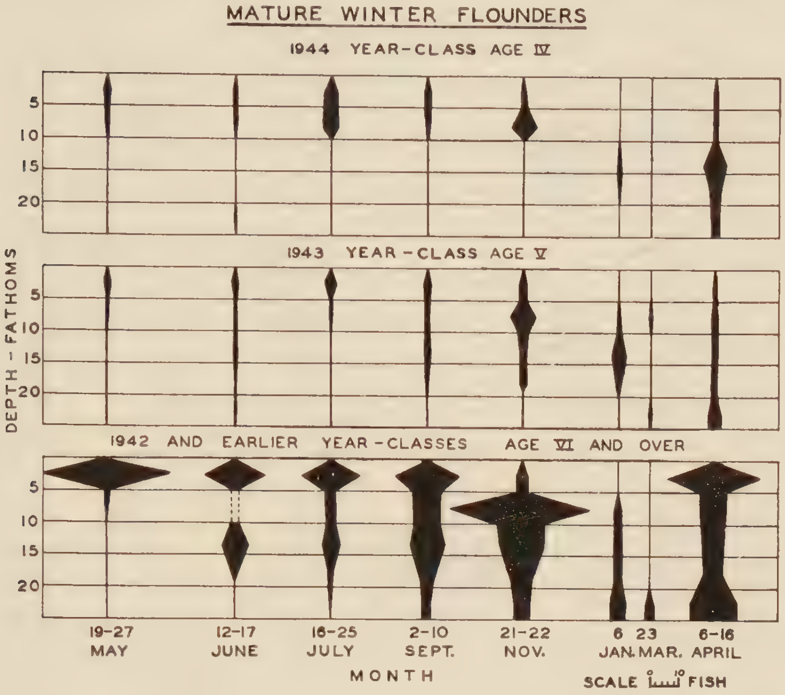

FIG. 4. Catch of mature winter flounders per 15-minute drag in Passamaquoddy Bay, by depth, age and month, during the period May 1947 to April 1948.

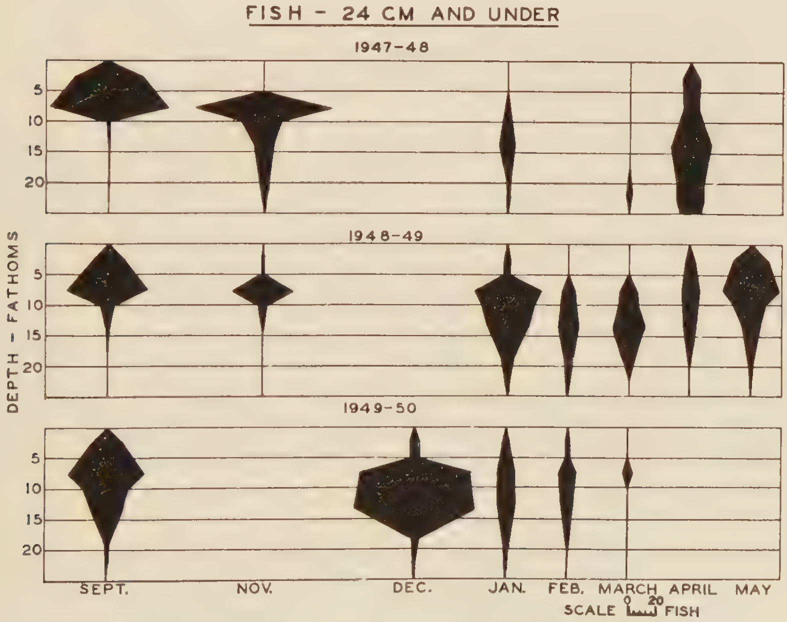

FIG. 5. Catch of winter flounders (24 cm and under) per 15-minute drag in Passamaquoddy Bay for the fall, winter and spring months, from 1947 to 1950, by month and depth.

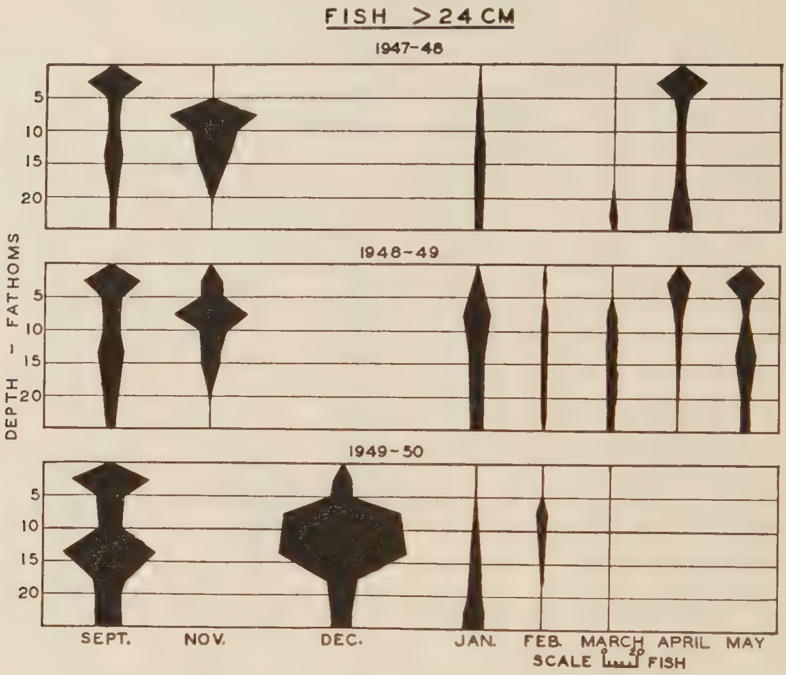

FIG. 6. Catch of winter flounders (> 24 cm in length) per 15-minute drag in Passamaquoddy Bay for the fall, winter and spring months, from 1947 to 1950, by month and depth.

CONSISTENCY OF SAMPLES. Throughout this study in Passamaquoddy Bay the same vessel, a standard 12-foot (3.6 m) beam trawl, and uniform trawling methods were used. Twice, a series of hauls were made in 5 to 10 fathoms (9–18m) at the same place at different times of day and night to test the consistency of catches. In the first series, June 15, 1949, paired hauls were made about midnight, sunrise, midafternoon and sunset. A similar series on August 17 and 18, 1949, began in midafternoon rather than midnight.

Analysis of the results (Tables II and III) by the chi-square method shows that mean size of fish did not differ significantly between hauls or time of day for either series. In six of the eight cases the number of fish taken in each tow of the pair did not differ significantly. The two cases of statistically significant variation occurred in the August series.

There is no consistent variation between numbers of fish taken at different times of the day but in both series the number of fish in the first pair of tows is significantly larger than the remainder of the series. Apparently the initial tows affected the subsequent availability of fish.

OCCURRENCE IN INTERTIDAL ZONE. Within Passamaquoddy Bay are large areas of intertidal flats, dry at low tide, which are outside the range of sampling reported above. Special efforts to sample these regions, (a) with the 12-foot (3.6 m) beam trawl, and (b) with a set seine, were made at irregular intervals.

TABLE II. Catch and mean length of fish for a number of tows at the same place in the 5- to 10-fathom (9–18 m) zone at different times of the day.

Date	Drag	Time of day	Code	Depth	Number of fish	Mean length
	no.			*fm*		*cm*
June 15/49	1	2400–0015	A	7–9	122	19.4
	2	0058–0112			121	19.2
June 15/49	3	0416–0431	B	6–8	84	18 6
	4	0449–0504			105	20.0
June 15/49	5	1405–1420	C	8–10	69	18.5
	6	1435–1450			82	20.1
June 15/49	7	1955–2000	D	5–7	96	19.7
	8	2018–2033			83	20.8

The χ^2 test of a 1:1 ratio gives the following approximate P values:

	Number of fish	Mean length		Number of fish	Mean length
Between A drags	P = 0.95	P = 0.95	A vs. B	P = 0.01	P = 0.99
Between B drags	P = 0.10	P = 0.50	A vs. C	P = 0.01	P = 0.50
Between C drags	P = 0.20	P = 0.50	A vs. D	P = 0.01	P = 0.50
Between D drags	P = 0.30	P = 0.50	B vs. C	P = 0.05	P = 0.50
			B vs. D	P = 0.50	P = 0.50
			C vs. D	P = 0.10	P = 0.50

Sampling with the beam trawl on five occasions yielded mostly large fish (Table IV). Greatest catch was in June 1947 and the smallest in November 1948.

Blocking off the intertidal zone in Brandy Cove with a set seine at irregular intervals between January and December 1949 caught flounders only between April and October (Table V), and not in winter and late fall. Fairly continuous sampling between mid March and mid May 1949 shows increasing numbers taken from early April to mid May. These data support those obtained in shallow-water stations by regular beam-trawl sampling to show increased abundance of winter flounders in the shore zone during spring and summer.

SEASONAL TEMPERATURE CYCLE AND CHANGES IN DISTRIBUTION. Mean monthly surface temperatures in Passamaquoddy Bay reach a maximum in August (averaging about 13°C in the period 1921–47) and a minimum in February (averaging 0.2°C in the period 1921–47) (Hachey and McLellan, 1948). During that time maximum mean surface temperature was recorded in August 1947 (14.8°C). Bottom temperatures at some depths where sampling was carried out between May 1947 and April 1948 are plotted in Fig. 7. Maximum temperature recorded was about 14.0°C, occurring in August and September in the shallowest water. From April to September shallow water was slightly warmer than the deeper, with a maximum bottom temperature difference of 2°C between 1 and 15 fathoms. By November the deeper water was slightly warmer than the shallow, although little temperature gradient existed.

Flounders moved into shallow water as warming to about 3 to 4°C occurred in spring and remained there all summer with temperatures up to about 14°C.

TABLE III. Catch and mean length of fish for a number of tows at the same place in the 5- to 10-fathom (9–18 m) zone at different times of the day.

Date	Drag	Time of day	Code	Depth	Number of fish	Mean length
	no.			*fm*		*cm*
Aug. 17/49	1	1354–1409	A	7–9	154	19.4
	2	1429–1444			103	18.7
Aug. 17/49	3	1840–1855	B	8–10	81	19.6
	4	1910–1925			72	20.7
Aug. 18/49	5	0035–0050	C	6–8	70	20.8
	6	0110–0125			64	19.2
Aug. 18/49	7	0535–0550	D	8–10	79	19.4
	8	0610–0625			56	20.4

The χ^2 test of a 1:1 ratio gives the following approximate P values:

	Number of fish	Mean length		Number of fish	Mean length
Between A drags	P = 0.01	P = 0.50	A vs. B	P = 0.01	P = 0.50
Between B drags	P = 0.30	P = 0.50	A vs. C	P = 0.01	P = 0.50
Between C drags	P = 0.50	P = 0.50	A vs. D	P = 0.01	P = 0.50
Between D drags	P = 0.05	P = 0.50	B vs. C	P = 0.20	P = 0.95
			B vs. D	P = 0.20	P = 0.95
			C vs. D	P = 0.95	P = 0.95

TABLE IV. Catch of winter flounders per drag with a 12-foot (3.6 m) beam trawl within the intertidal zone.

Date	Number per drag	
	Small	Large
	24 cm and less	*Over 24 cm*
May 13, 1949	1	10
June 17, 1947	4	44
July 18, 1947	2	21
August 20, 1948	1	16
November 30, 1948	0	2

TABLE V. Catch of large and small winter flounders in a set seine in Brandy Cove.

Date	Number of fish			
	Small		Large	
	Total	No. per day fished	Total	No. per day fished
	24 cm and under		*Over 24 cm*	
Jan. 7, 1949	0	0	0	0
Jan. 24, 1949	0	0	0	0
Jan. 27, 1949	0	0	0	0
Feb. 10, 1949	0	0	0	0
Feb. 22, 1949	0	0	0	0
Mar. 14–16, 1949	0	0	0	0
Mar. 28–31, 1949	0	0	0	0
Apr. 4–9, 1949	0	0	10	3.3
Apr. 10–17, 1949	3	0.4	31	4.4
Apr. 19–25, 1949	6	1	27	4.5
Apr. 26–30, 1949	32	6.4	66	13.2
May 1–11, 1949	90	9	203	20.3
Oct. 12–15, 1949	108	36	33	11
Nov. 8, 1949	0	0	0	0
Nov. 30, 1949	0	0	0	0
Dec. 23, 1949	0	0	0	0
Jan. 23, 1950	0	0	0	0

They moved out of the shallows in fall as the deeper water became warmer than the shallows. Temperatures at that time in fall were about 6 to 7°C in the shallows, considerably higher than the temperature level at which flounders moved into the shallows in spring.

Minimum catch-per-effort of flounders in the Bay coincided with minimum water temperatures, February–March in 1948. The winter of 1949 was warmer than either that of 1948 or 1950, and catch per effort was higher during that year than in either of the others.

Sampling in other Canadian areas has determined the distribution of winter flounders in St. Mary Bay and Pubnico Harbour region, N.S., and in Northumberland Strait (Fig. 1). While sampling was less extensive than in Passamaquoddy Bay, records of small commercial fisheries in these regions and tagging in St. Mary Bay have helped outline distribution there.

ST. MARY BAY, N.S.

St. Mary Bay (Fig. 1 and 8) is a long, gently shelving bay emptying westward into the southern side of the mouth of the Bay of Fundy. It is about 30 miles (48 km) long and varies in width from 10 miles (16 km) at the mouth to 4 miles (6.5 km) at the inner end. The depth of water ranges from 22 to 25 fathoms (40–46 m) at the mouth to extensive tidal flats at the head. The Bay is separated from the Bay of Fundy by a long, narrow neck of land, Digby Neck,

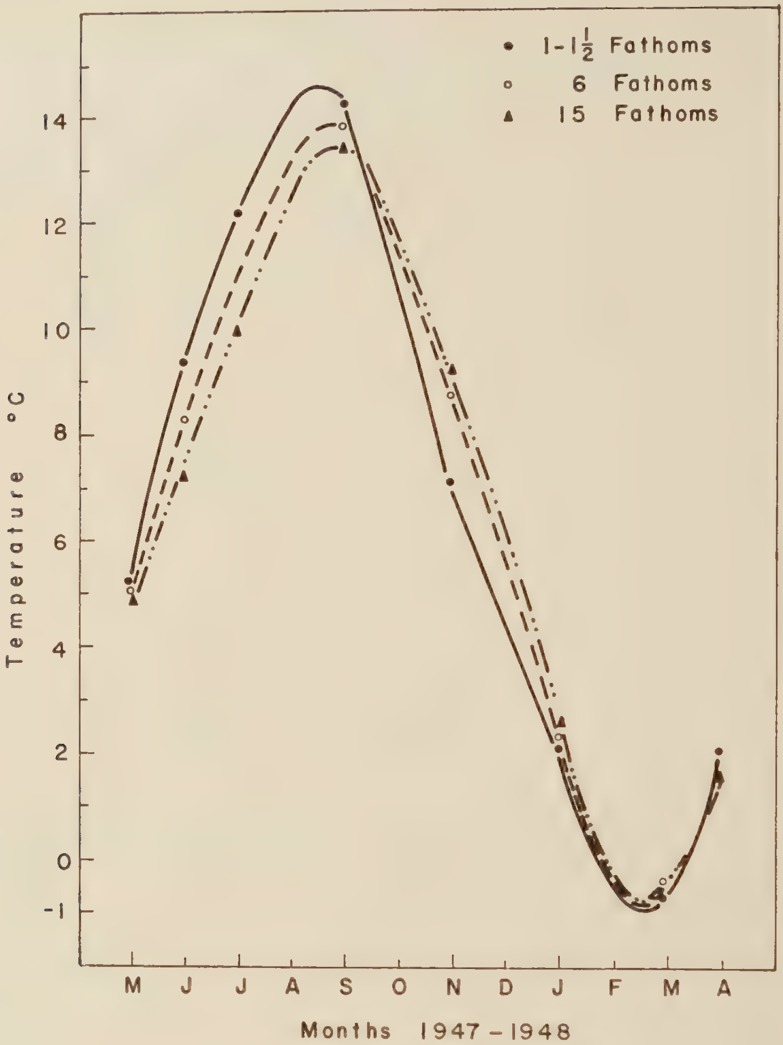

FIG. 7. Bottom temperatures at sampling stations in Passamaquoddy Bay at the time of dragging.

rising abruptly from the water. To the southeast it is bounded by the mainlan of Nova Scotia where the coastline is indented by numerous shallow coves an is characterized by gently sloping sand or mud beaches and tide flats.

Results of exploratory flounder fishing and the subsequent flounder fisher on the Nova Scotia side of the Bay of Fundy have been described by McCracke and Martin (1950). Following exploratory fishing in St. Mary Bay one sma dragger was granted an "experimental" commercial dragging licence to fish ther in 1948. A rapid expansion followed in 1949 with about 15 small dragge fishing St. Mary Bay. Peak effort for winter flounders was reached in 1950–5 Subsequently the draggers fishing there began fishing for haddock (*Melanogram*

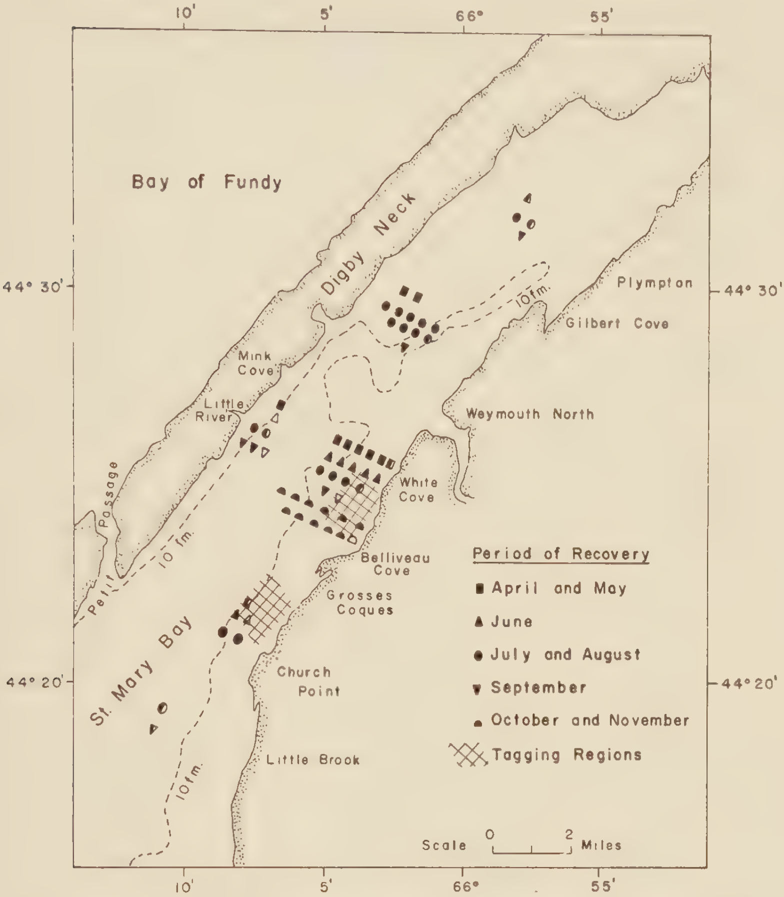
Bay of Fundy
Digby Neck
Mink Cove
Little River
Petit Passage
10 fm.
St. Mary Bay
Plympton
Gilbert Cove
Weymouth North
White Cove
Belliveau Cove
Grosses Coques
Church Point
Little Brook
Period of Recovery
■ April and May
▲ June
● July and August
▼ September
▲ October and November
Tagging Regions
Scale 0 2 Miles
10'
5'
66°
55'
44° 30'
44° 20'

FIG. 8. Number of tag recoveries and region of recovery by 10 small draggers in 1950 from tagging in October and November 1949. Each completely shaded symbol represents 5 recoveries.

mus aeglefinus) and wolffish (*Anarhichas lupus*) as well as flounders, according to season and availability. Operators of draggers were required to keep records, and these provide information about the distribution and seasonal changes in the fishery. These changes can be related to the distribution of winter flounders in the Bay. Best records were obtained in the first few years of the fishery, and these have been used for the following comparisons.

Records of the fishery show that dragging began in the last week of March in 1949 and 1951 and in the first week of April in 1950. Dragging ceased in late October in 1948 and about mid November in 1949 to 1951. Catch records for 1950 (Table VI) show the proportion of the landings taken throughout the season of 1950 and the catch per hour dragged. Records have been divided for vessels using a 50-foot net and those using a 40-foot net, roughly a division into large and small vessels.

TABLE VI. Proportion of St. Mary Bay winter flounders landed during various periods in 1950.

Period	Large draggers		Small draggers	
	%	*lb/hr*	%	*lb/hr*
Winter	0	0	0	0
April	19	225	0	178
May	34	240	8	145
June	24	185	37	125
July–August	18	130	30	95
Fall (to mid November)	5	...	25	116[a]
Total landings (1000 lb)	459		812	

[a]Includes a marked increase in late October to just over 200 lb per hour.

The start of the larger boat fishery in spring was controlled apparently by the low availability of flounders prior to early April. In interviews, fishermen have reported trials in mid March which either yielded few flounders or none at all. Data in Table VI show that the larger draggers dropped out of the fishery in mid summer as catch per effort was reduced. Small boats continued fishing flounders into fall but converted to the more lucrative lobster fishery of the region in November. Interviews with fishermen indicate that winter flounders are present in the Bay after fishing ceases in mid November.

Tagging carried out in St. Mary Bay during the fall of 1949 and in the spring and fall of 1950 was partly designed to determine fishing rates (Dickie and McCracken, 1955) and to help determine distribution and movements of St. Mary Bay flounders. Approximately 2,600 flounders were tagged with a modified Petersen disk in 1949 and 3,500 in 1950. Total recaptures from the fall tagging of 1949 and 1950 were about 35 and 25%, respectively. Recaptures from the spring tagging in 1950 were higher, about 60%.

Tag recoveries show the general pattern of winter flounder distribution within the Bay during the fishing season, although results were limited by lack of winter recaptures and the precision in determining place and depth of recapture. Recaptures from the 1949 fall tagging, reported by operators of 10 small draggers keeping good records, during the fishing season of 1950 are presented in Fig. 8. Tagged fish were retaken throughout the Bay with largest numbers recovered in the regions where catch and effort were greatest. Recoveries were lowest outside Church Point and off Gilbert Cove at the head of the Bay. Largest numbers were reported about mid Bay, off White and Belliveau Coves. With only one or two exceptions, all recaptures have come from inside the Bay.

Some fish tagged off Church Point in May 1950 had moved to the head of the Bay by June. Largest recoveries from this tagging were from the Weymouth and White Cove region. It is thus apparent that flounders dispersed into the Bay after tagging in May.

PUBNICO HARBOUR, N.S.

Pubnico Harbour is a shallow bay about 7 miles (11 km) long and up to 1½ miles (2½ km) wide (Fig. 1). Most of the bay is shallow-water flats covered with water to a depth of about a fathom (2 m) at low tide and about 2½ fathoms (4½ m) at high water. A channel about ⅕ of a mile (0.3 km) wide and about 5–10 fathoms (9–18 m) deep extends into the bay for most of its length.

Reports of local handlining of winter flounders for lobster bait indicated that they were available in Pubnico Harbour by early April and that catches were much reduced by late May (Table VII). Since the lobster fishing season closes there by the end of May, the reduced catches of flounders in late May were insufficient evidence that they were no longer available. However, results of exploration carried out in Pubnico Harbour in 1948 confirm that flounders were much reduced by June.

Table VIII presents the results of beam-trawl hauls in Pubnico Harbour in May, June, July and October 1948. Abundance of both immature and mature winter flounders decreased markedly between May and June. Between June and July abundance in the shallows decreased still further but catches of both immature and mature fish increased in mid-harbour channel.

Catch of immatures per drag in October was about the same as in July, while matures had practically disappeared. At the mouth of the harbour catches of immatures were relatively high in May but had decreased markedly by June, but after that time no trend is apparent. Catches of matures show a downward trend throughout the season.

TABLE VII. Landings of winter flounders from the Pubnico Harbour region, by month and year.

Year	Jan.–Mar.	Apr.	May	June	July	Aug.–Dec.
	cwt	*cwt*	*cwt*	*cwt*	*cwt*	*cwt*
1947[a]	—	—	—	—	—	—
1948	Nil	300	879	8	Nil	Nil
1949	Nil	397	635	Nil	Nil	Nil
1950	Nil	150	436	Nil	Nil	Nil
1951	Nil	50	35	8	4	Nil
1952	Nil	120	766	20	Nil	Nil

[a] Not reported for 1947; local Fisheries Officer indicates that there were landings in April and May but quantity unknown.

TABLE VIII. Catch of winter flounders per 15-minute tow in Pubnico Harbour, 1948.

	Head of harbour intertidal 5 fathoms			Channel–mid harbour 6–8 fathoms			Mouth of harbour 7–9 fathoms		
Month	Immature	Mature	Total	Immature	Mature	Total	Immature	Mature	Total
	no.	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*
May	35.1	24.0	59.1	56.6	5.5	62.1	13.5	1.8	15.3
June	6.4	5.7	12.1	9.0	1.0	10.0	4.8	0.5	5.3
July	3.2	3.5	6.7	17.6	7.3	24.9	3.2	0.8	4.0
Oct.	0.3	...	0.3	15.3	...	15.3	3.9	...	3.9

On the outer coast, just west of Pubnico, at East Tusket, catches of flounders in June were much higher than in Pubnico Harbour. At a depth of about 2–4 fathoms (4–7 m) average catch per tow was about 34 immature and 14 mature winter flounders. Catches at comparable depths in Pubnico Harbour were about 6 per tow for both immature and mature winter flounders.

Temperatures of the shallow water of Pubnico Harbour, extending over large mud flats, increase much faster and reach higher levels than on the outer coast. Temperature records at various depths are shown in Table IX. The reduction in abundance of winter flounders in the Harbour occurred by the time temperatures on the flats were reaching 13–14°C in June. At East Tusket the temperature at similar depths, 3–5 fathoms (5–9 m), was about 11°C. Since catches in deep water outside Pubnico Harbour during June and July had not increased, it is suggested that flounders moving out of Pubnico Harbour remained in shallow but cooler waters of the open coast.

TABLE IX. Water temperatures in Pubnico Harbour during May, June and October 1948.

Date	Depth	Intertidal temp.	Channel temp.	Mouth of harbour temp.
	fm	°*C*	°*C*	°*C*
May 3–4	0.66	8.7		
	1.5	8.0		
	2	7.0		
	5		6.3	
	12			4.4
May 19–21	Surface	10.7–10.5		
	0.66	10.5–10.3		
	1.5	9.7		7.1–7.2
	5	7.6–8.2		6.3–6.1
	8			5.8
	11			4.8
June 14–16	Surface	14.3–13.5		
	0.66	14.0–13.7		
	1.5	11.7–11.2		7.7–7.9
	5	10.0		
	8			7.1
	11			7.0
Oct. 28–29	1.5	9.8		
	5	10.0		10.5–10.8
	8			10.5
	11			10.7

NORTHUMBERLAND STRAIT

Northumberland Strait in the southern Gulf of St. Lawrence separates Prince Edward Island from the mainland of New Brunswick and Nova Scotia (Fig. 1). Exploration was carried out mainly toward the eastern end of the Strait. In general, depth increases gradually and in the area explored the 10- and 20-fathom (18 and 36 m) depth contour lies well offshore.

Exploration throughout the southern Gulf of St. Lawrence has shown the winter flounder to be common there (McCracken and Martin, 1950). Distribution in relation to depth in the eastern Northumberland Strait, off Murray Harbour, P.E.I., and Pictou, N.S., in August 1947 and 1952 is shown in Fig. 9. In 1947 catch per drag was small at depths less than 6 fathoms (11 m) and greatest between 7 and 10 fathoms (13 and 18 m). At 7 to 10 fathoms flounders taken were less than commercial size (30 cm). In deeper water, 12 to 15 fathoms (22–27 m) fish were mainly over 30 cm in length but total numbers were somewhat less than at intermediate depths.

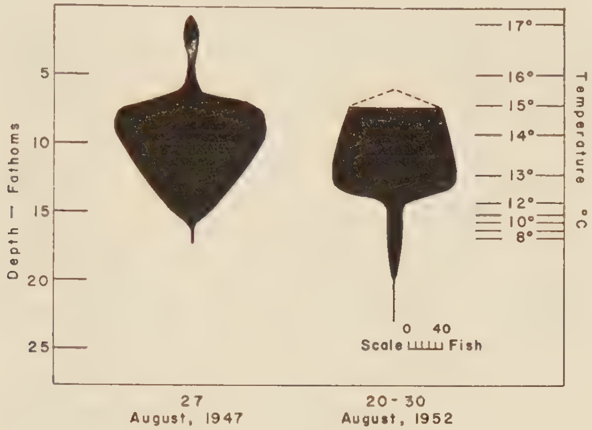

FIG. 9. Distribution of winter flounders in eastern Northumberland Strait in relation to depth and temperature.

In 1952 a series of drags between 8 and 23 fathoms (15 and 42 m) took large numbers of flounders down to about 15 fathoms (27 m). No dragging was carried out at depths less than 8 fathoms (15 m).

Temperatures were not taken during exploratory dragging in August 1947 but Lauzier (1948) shows that in late August 1947 in this area temperatures ranged between 18°C at the surface and 14°C at 11 fathoms (20 m). The temperature at bottom where dragging was carried out in 1952 was taken along with surface layer temperatures. These have been combined in the temperature scale shown in Fig. 9. Temperatures were about the same in both 1947 and 1952. Catches of winter flounders in 1947 were greatest in water temperatures above about 12°C and below 16°C. Catches in 1952 were low at depths with temperatures less than 12°C, and probably in the shallow, warm water as well.

In August there was also a marked change in size of fish with depth (Fig. 10). Between 8 and 10 fathoms (15 and 18 m) fish over 30 cm (commercial size) made up a small proportion of the total while at 12 fathoms (22 m) a large proportion of the catch was large fish over 30 cm. In this same area in late October and early November the gradation of size with depth had disappeared. Large fish, over 30 cm, had spread into shoaler water and intermediate sizes, 20-29 cm,

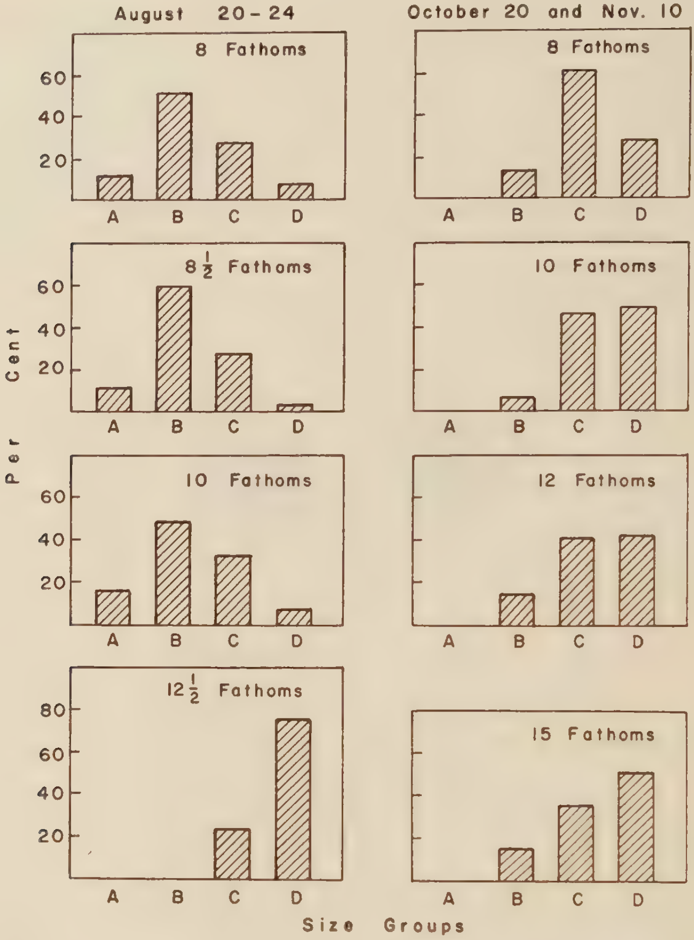

FIG. 10. Percentage size composition of winter flounders by depth in eastern Northumberland Strait. Size-groups are: A = 10–19 cm; B = 20–24 cm; C = 25–29 cm; D = 30 cm and over.

had moved into deeper water. In contrast to August conditions, the water was almost isothermal from surface to bottom at this time (about 14°C on October 27 and 12°C on November 10).

Off Souris, P.E.I., catches with a 12-foot (3.6 m) beam trawl in July 1947 were greatest in shallow water, about 15 fish per tow in 2–3 fathoms (4–6 m). In September of that year shallow-water catches were nil and largest catches were obtained in deeper water, about 10 fish per haul in 12–15 fathoms (22–27 m).

Winter flounders are fished in Northumberland Strait in spring in shallow water for lobster bait. According to local fishermen, they are taken by hoop traps and those taken are mainly larger, mature fish. A small, localized, dragger fishery which developed near the western end of Northumberland Strait off Richibucto and Escuminac, N.B., has relied on inshore, spring concentrations of winter flounders at depths less than 5 fathoms (9 m). As the season progresses, the fishery ceases as the result of much reduced catches in the shallow water.

These data support the conclusion that winter flounders are found in the shallow, inshore waters of Northumberland Strait during spring and early summer months. By mid summer catches in the shallows are much reduced and flounders are most abundant at intermediate depths, 8–13 fathoms (15–24 m). Flounders move out of the shallow water as temperatures increase there and the concentration of winter flounders in mid summer occurs between temperatures of 12° and 15°C.

In summary, there is evidence for Passamaquoddy Bay and fairly good evidence for St. Mary Bay that winter flounders leave the shallows in winter, moving to nearby deeper water. Probably winter flounders are also absent from the shallows in Northumberland Strait and the Pubnico Harbour region during winter. In spring, winter flounders are found in the shallows for all regions sampled in the Canadian area. In summer there is a difference in distribution of winter flounders between the cool-water areas, Passamaquoddy Bay and St. Mary Bay, and the warm-water areas, Pubnico Harbour and Northumberland Strait. In the former, winter flounders are abundant in shallow water during the summer; in the latter they leave the warm shallows and are found in the deeper, cooler water as in Northumberland Strait, or the cooler, shallow water of the exposed coast off Pubnico.

Relating temperature with summer distribution in these regions shows that winter flounders leave areas of temperature above 14–15°C and tend to remain at depths where temperature is above 12°C when temperatures around 12–15°C are available.

United States Regions

Movements of winter flounders have been well documented for the region around Long Island, N.Y., where a study of their distribution has been carried out in relation to sport and commercial fisheries there and reported by Lobell (1939). Short-term studies carried out in Block Island Sound (Merriman and Warfel, 1948) and by tagging off southern New England (Perlmutter, 1947) have also outlined seasonal changes in distribution. For the region further north, off Cape Cod, statistics of the commercial fishery have been used in this paper to deduce seasonal changes in distribution.

Table X. Temperatures (°C) for Great South Bay and the outer coast of Long Island (summer 1938) and average depth at temperature stations (from Perlmutter, 1939).

Place	Depth	Date and temperature				
		June 14–16	July 26	Aug. 8	Sept. 7	Oct. 4
	fm	°*C*	°*C*	°*C*	°*C*	°*C*
Great South Bay	1	20	24	. . .	21	15
Outer coast	4	12	. . .	16	18	17

In this study temperature records from a variety of sources were correlated with winter flounder distribution records off New England, and added to the information obtained from the investigation in the Canadian region.

LONG ISLAND WATERS AND BLOCK ISLAND SOUND. For this region of relatively shallow bays, the distribution and movements of winter flounders have been documented by Lobell (1939) and Merriman and Warfel (1948) from tagging results, studies of commercial and sport catches and by special sampling from the commercial fleet.

TABLE IX.A. Catch of winter flounders per day's fishing by otter trawl, by month, in Peconic Bay and Gardiner's Bay, Long Island (from Lobell, 1939).

	Catch per day's fishing	
Month	Peconic Bay	Gardiner's Bay
	lb	*lb*
Jan.	189	no effort
Feb.	184	80
Mar.	295	320
Apr.	250	470
May	275	540
June	no effort	670
July	no effort	105
Aug.	no effort	45
Sept.	no effort	50
Oct.	no effort	70
Nov.	no information	no information
Dec.	no information	no information

TABLE XI.B. Average monthly bottom temperature (°C) and average depth in Gardiner's–Peconic Bay region for the year 1938 (from Perlmutter, 1939).

Place	Average depth	Month and average bottom temperature				
		May	June	July–Aug.	Sept.	Oct.
	fm	°*C*	°*C*	°*C*	°*C*	°*C*
Peconic Bay	2.3	15.3	21.5	25.7	20.5	14.8
Mouth of Peconic Bay	3.3	14.8	19.1	25.2	20.4	14.6
Gardiner's Bay	3.1	13.3	17.5	22.8	19.7	14.3
Mouth of Gardiner's Bay	5.5	11.5	15.4	19.0	18.4	14.7
Montauk Point	6.8	11.2	13.3	16.2	17.2	15.8

Lobell (1939) shows from tag recoveries and catch records of the commercial fleet in 1938 that in one of the Long Island bays (shallow Great South Bay on the outer coast), flounders leave the Bay by May, but remain just outside during the summer months. Comparison of these results with temperatures reported by Perlmutter (1939) suggests that flounders moved out of the Bay before temperatures reached 20°C (Table X), but remained near shore in the cooler waters of the outer coast.

Lobell (1939) shows a more complete and precise pattern of the seasonal distribution of winter flounders during 1938 in a series of bays (Peconic, Gardiner's and Block Island Sound) which open one into the other. Catch and effort were high in the inner, shallower Peconic Bay during January and February, in both Peconic and Gardiner's Bay (the middle Bay) in March, and almost completely confined to Gardiner's Bay by May (Table XI. A). The occasional effort recorded from July to September was in the mouth of Gardiner's Bay at its entrance to Block Island Sound. Comparison of these results with temperatures reported by Perlmutter (1939) for this region (Table XI. B) shows that the fishery ceases in each of the areas sometime during the month that average bottom temperatures reach 13–14°C.

Merriman and Warfel (1948) record that commercial fishing for winter flounders was mainly from deeper water, around 20 fathoms (37 m) from June

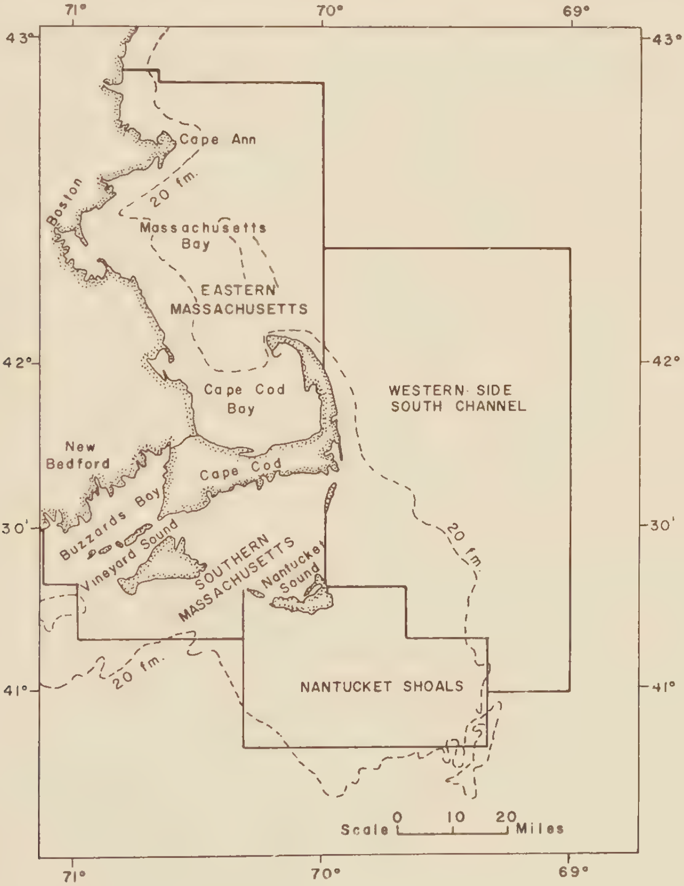
71°
70°
69°
43°
42°
30'
41°
Cape Ann
Boston
20 fm.
Massachusetts Bay
EASTERN MASSACHUSETTS
Cape Cod Bay
WESTERN SIDE SOUTH CHANNEL
New Bedford
Cape Cod
Buzzards Bay
Vineyard Sound
SOUTHERN MASSACHUSETTS
Nantucket Sound
NANTUCKET SHOALS
Scale 0 10 20 Miles

FIG. 11. Statistical subareas in the vicinity of Cape Cod (adopted in 1939 by the North American Council on Fisheries Investigations).

to September, and shallower water, 10 to 15 fathoms (18–27 m), during the remainder of the year. The temperature data presented by Merriman and Warfel (1948) indicate that winter flounders leaving the bays at the eastward end of Long Island move into waters of less than 15°C.

CAPE COD REGION. Statistics of the commercial landings of winter flounders from just north and south of Cape Cod, Massachusetts, present an interesting contrast and seem capable of interpretation as differences in seasonal movements of winter flounders in the two regions. Just south of Cape Cod (Fig. 11) the 20-fathom contour extends well offshore and the large shoals off Nantucket Island are mainly less than 10 fathoms (18 m), while north of Cape Cod the 20-fathom contour is closer to shore than in the area south of Cape Cod. Practically the total catch of winter flounders is taken by otter trawlers, classed as "small" (50 gross tons or under), "medium" (51–150 gross tons), "large" (151 gross tons or greater).

In the inshore subarea "Southern Massachusetts" (Fig. 11) during 1951, for example, catches were all taken by small otter trawlers, and peak catch per effort was obtained in April and May (Fig. 12). Catch per effort dropped markedly in June and by July and August winter flounders were virtually absent from the catches there. By November catch per effort had increased markedly.

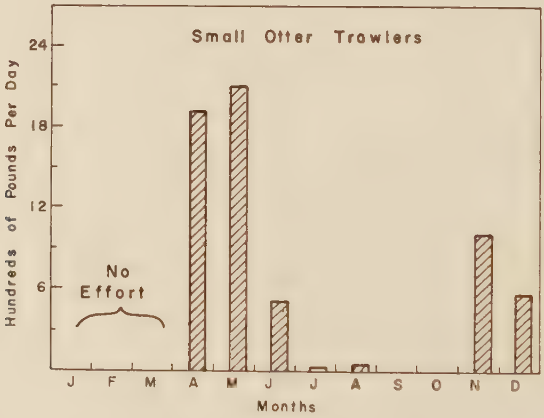

FIG. 12. Catch of winter flounders per day's absence from port, by months, for "small" otter trawlers for the year 1951 from southern Massachusetts. (From U.S. Fish and Wildlife Circulars — Massachusetts Landings.)

In the subarea "West Side of South Channel", lying along the outer part of Cape Cod, all three sizes of otter trawler operated throughout the year. Winter flounder catch per effort for "small" trawlers was at a minimum in February and March, increased in April and reached a maximum in June (Fig. 13). Catch per effort decreased after June, reached a second low in September, then increased in October through December. Catch per effort for "medium" trawlers was at a low level from January through April but increased from May to a maximum

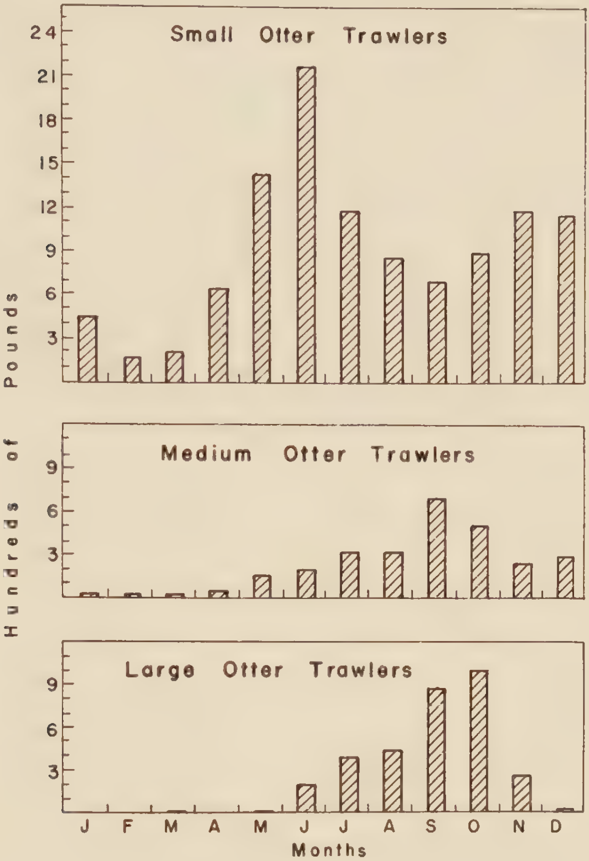

FIG. 13. Catch of winter flounders per day's absence from port, by months, for "small", "medium" and "large" otter trawlers for the year 1951 from "West Side of South Channel". (From U.S. Fish and Wildlife Circulars — Massachusetts Landings.)

in September, then decreased from October through December. "Large" trawlers first caught winter flounders in June and catch per effort increased steadily to a maximum in October, followed by a sharp drop in November and December.

For the Massachusetts Bay region catch per effort for both small and medium otter trawlers was greatest in the winter months, about December to March, and lowest from April through October.

Tagging results for the Cape Cod region reported by Perlmutter (1947) show little mixing between winter flounders from south of Cape Cod and those north of Cape Cod. The results show local movements but unfortunately recaptures are not reported by depth and season.

The most logical interpretation of changes and differences in catch per effort for these regions is that they are related to inshore–offshore movements of winter flounders. The drop in catch per effort by June in the inshore "Southern Massachusetts" area occurs as catch per effort reaches a peak in the more offshore "West Side of South Channel" area. The catch-per-effort pattern for large trawlers in the latter area suggests that in summer flounders continue moving into deeper, offshore waters where these large vessels would be expected to fish.

The low catch per effort in summer north of Cape Cod (Massachusetts Bay) contrasts directly with the situation south of Cape Cod. Since catch per effort was high in winter in Massachusetts Bay, the most logical explanation is that during summer winter flounders are in the shallow, inshore water. High catch per effort in winter north of Cape Cod also contrasts with the low catch per effort south of Cape Cod. The logical conclusion is that winter flounders are found offshore in winter, north of Cape Cod, but inshore south of Cape Cod. Distribution north of Cape Cod appears more like that of the Bay of Fundy, while that south of Cape Cod appears more like that of the Long Island region.

LABORATORY STUDIES

Lethal Temperature

During this study various attempts were made to determine a preferred temperature for winter flounders. Several types of apparatus were used to set up horizontal temperature gradients but flounders failed to react by selecting any particular portion of these gradients. In addition, an attempt was made to determine swimming speed of winter flounders in relation to temperature in the manner described by Fry and Hart (1948). Rotation of the annular chamber failed to elicit any steady swimming rates and the experiment was abandoned. Only upper lethal temperature for flounders was determined.

Flounders were acclimated at five temperature levels, maintained to within ±0.5°C. All acclimations were to increased temperatures and following the procedures of Fry *et al.* (1946) at least one day per degree of temperature difference was allowed for thermal adaptation. Fish were fed on chopped clams throughout holding and acclimation. The lethal temperature method was similar to that described in various papers by Fry *et al.* (1942, 1946, 1947). Water in the lethal baths was maintained at a constant temperature (±0.3°C), renewed at approximately 200 cc per minute and aerated by compressed air.

Observations were continued for at least 24 hours in all tests, and occasionally for 72 hours. The percentage of fish surviving a given temperature at the end of 24 hours was calculated and the temperature at which 50% of the fish survived for 24 hours was found by interpolation from the survival curves.

Such arbitrary termination of lethal tests was questioned by Doudoroff (1945), and Fry *et al.* (1946) showed that to delimit the zone of resistance exactly the test should be continued until a break occurs in the straight-line plot of the logarithm of time to 50% mortality against temperature in the lethal range. When tests are continued beyond 24 hours mortalities keep on, so the estimate of the zone of tolerance is high. It appears adequate, however, to relate the zone of tolerance with the temperatures likely to be encountered by this species.

The relationship between the temperature of acclimation and the upper level of temperature that 50% of the flounders tested could tolerate for 24 hours is presented in Fig. 14. Upper lethal temperatures range from about 19°C for fish acclimated at 4°C to about 26.5°C for fish acclimated to temperatures 20°C and over. The ultimate upper incipient lethal temperature is about 27°C.

Temperatures in Canadian waters do not reach lethal levels even in the warmest bays, such as Malpeque Bay, P.E.I., where Needler (1931) reported maximum temperatures of 22–23°C. However, mortality attributed to high temperatures has been reported by Nicholls (1918) for Moriches Bay, Long Island, in late July 1917. Water temperatures were not recorded but in this extremely warm spell mean daily air temperatures at New York reached 29–32°C.

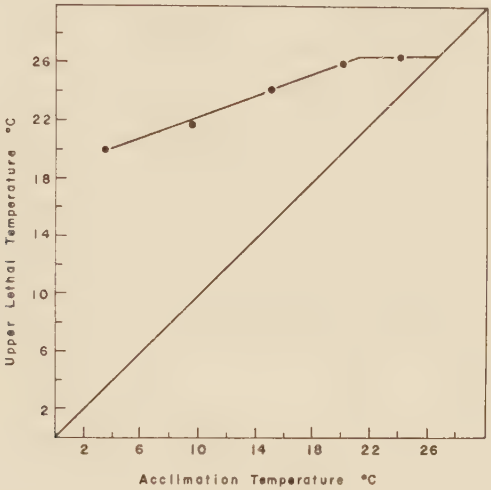

FIG. 14. The relation between acclimation temperature and the upper lethal temperature for the winter flounder. (Lethal test period — 24 hours.)

REACTIONS TO LIGHT

A characteristic reaction of "disturbed" winter flounders is to flutter the fins so that a covering of sand or mud is spread over the body. After slight fluttering the body is only partially covered, while in the more pronounced reaction the fish settles in the hollow created by its fluttering and is almost completely covered with sand. When buried, the fish does not move readily, and often can be removed from the sand or mud before movement occurs.

A burying reaction will occur in experimental tanks where no covering material is available, and Mast (1916) indicates that with the flounder, *Paralichthys dentatus* (L), the reaction will continue to occur for at least several months. Preliminary observations under experimental conditions showed that winter flounders which had been in darkness would, if suddenly exposed to light, respond by attempting to bury. If no sand was available they would, on continued exposure, move around the tank, and if a portion of the tank was shaded, some of the fish tended to congregate there. Andrews (1946) has termed such movement from light to shade a "cover response".

These preliminary observations also indicated differences in reaction between sizes of fish, and a series of experiments in the winter of 1948 was designed to provide a more quantitative assessment of the reaction of winter flounders to exposure to light sources of different intensities.

Two different experiments were carried out. In one series a wooden tank 4 feet long by 18 inches wide and containing water of about 5 inches deep was used. The top of the tank was covered with a tarpaper shield so arranged that either half could be lifted, thus exposing the portion of the tank below. The light source used was suspended 4½ feet above the water level, directly over the middle of the tank. The light source was either a 100-, 50-, 25- or 7½-watt unfrosted light bulb.

Small (6–9 cm), intermediate (12–18 cm) and large (28–33 cm) flounders were used. Five fish of one size category were marked so they could be easily distinguished and placed in the tank for 24 hours before light tests were done. The light was turned on and half the tank was exposed to the light by removing the cover from that half. The cover was removed from opposite halves of the tank alternately in a series of exposures.

Reaction of the fish to the light stimulus was slow and, as a result, observations after each exposure were carried out for a considerable period of time. Length of exposure was noted. Between exposures fish were left in darkness for a period of not less than 3 hours.

TABLE XII. Number of fish in the exposed portion of an experimental tank at the beginning and end of exposure to a light source; exposure time one hour. (The possible number of occurrences was 45 with the 100-watt bulb and 40 with each of the other sources. Statistical procedure used was the "t" test for paired values (Goulden, 1939).)

	Large fish			Intermediate fish			Small fish		
Light source	Beginning	End	P value	Beginning	End	P value	Beginning	End	P value
100-watt bulb	32	16	<0.01	28	2	<0.01	24	17	>0.05
60-watt bulb	23	12	<0.01	29	2	<0.01	15	29	<0.01
25-watt bulb	16	21	>0.5	25	9	<0.01	21	34	<0.05
7½-watt bulb	18	19	>0.5	24	12	<0.01	16	27	<0.01

Even though the tank bottom was bare, a sudden exposure to light brought about the characteristic fluttering of the fins. Movement into the shade was not immediate, but after continued exposure a statistically significant change in the number of fish in the uncovered portion of the tank occurred (Table XII) in some instances.

Large fish moved out of the light when exposed to the 100- or 60-watt light sources, while with the 25- and 7½-watt sources no statistically significant changes in distribution were found. For intermediate-size fish the change in distribution was statistically significant with all light sources used as they moved into the shade. The change in distribution of small fish exposed to the 100-watt light source is not significant at the 5% level but there is an indication that they moved into the shade. With all other light sources, small fish increased in number in the lighted portion of the tank and the change in number is statistically significant.

In the second series of experiments the same tank and light sources were used, but about 1 inch of sand was placed on the bottom of the tank. The top of the tank was left uncovered although between exposures the room was in darkness. The fish used were of the same sizes outlined above.

Sudden exposure of winter flounders to light in a tank with sand on the bottom often produced an immediate and pronounced burying reaction, which, because it caused turbidity, made observation difficult. Also, close inspection was needed to reveal the location of buried fish. To facilitate observations only two fish of each size were used in a given experiment.

Observations on the number of each size of fish buried after 10 minutes exposure to light of the four light sources are shown in Table XIII. All four light sources stimulated a statistically significant number of burying reactions for all three size categories of fish.

TABLE XIII. Number of fish unburied in a tank with the sand on the bottom. The tank was completely exposed to light. Results shown are for 10-minute exposures. (Two fish of each category were used for each exposure. The burying reaction was considered to have taken place if the eyed surface of the fish was at least partially covered with sand. Statistical procedure used was the "t" test for paired values (Goulden, 1939).

	Large fish			Intermediate fish			Small fish		
	Unburied			Unburied			Unburied		
Light source	Beginning	End	P value	Beginning	End	P value	Begining	End	P value
100-watt bulb	19	5	<0.01	16	3	<0.01	24	9	<0.01
60-watt bulb	20	7	<0.01	18	4	<0.01	19	8	<0.01
25-watt bulb	16	4	<0.01	16	3	<0.01	21	9	<0.01
7½-watt bulb	18	6	<0.01	15	3	<0.01	20	12	<0.02

DISCUSSION

FACTORS AFFECTING "SUMMER" DISTRIBUTION

TEMPERATURE. Since the winter flounder proved to be unresponsive to thermal stimuli in the laboratory, the effect of temperature on its distribution was deduced from comparison of similarities and differences over a wide geographic range.

The occurrence of winter flounders from April through November in Peconic Bay and Gardiner's Bay in Long Island, Passamaquoddy Bay and at three different depths in Northumberland Strait in relation to temperature is illustrated schematically in Fig. 15. Winter flounders were abundant in Peconic Bay in early spring but by mid May as temperatures reached about 15°C flounders

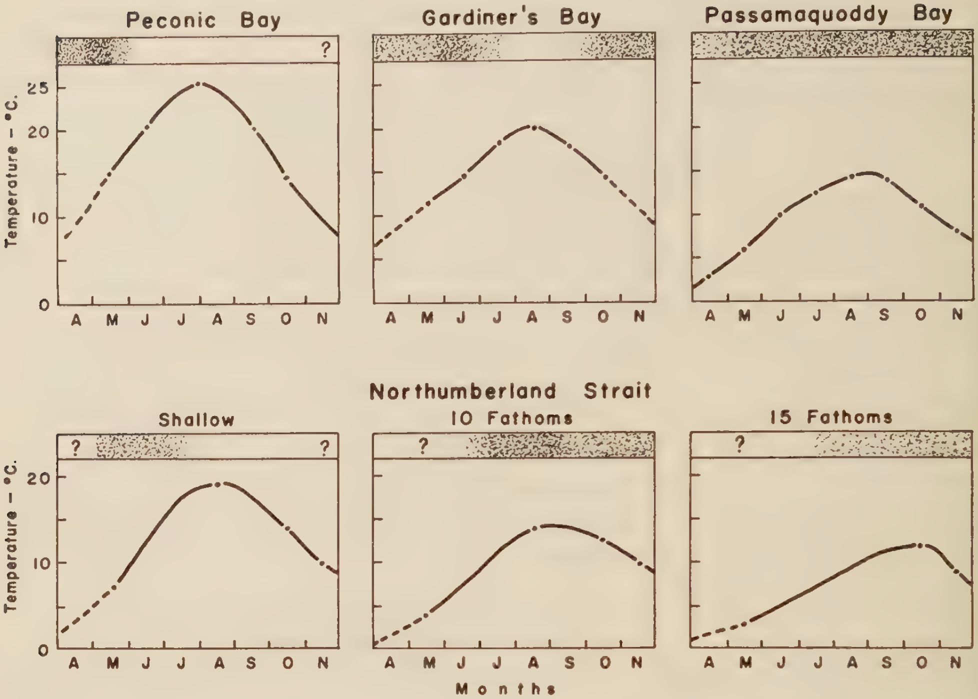

FIG. 15. Schematic presentation of the occurrence of winter flounders in relation to temperature for 4 areas, from data presented previously in detail. In the horizontal bars the degree of shading indicates the relative abundance of winter flounders.

were no longer caught. Winter flounders were no longer caught in Gardiner's Bay as temperatures increased above 15°C but this stage was reached much later, late June, than in Peconic Bay. Winter flounders increased again in numbers in Gardiner's Bay in October as water temperatures decreased to about 15°C.

In contrast, winter flounders were abundant in Passamaquoddy Bay shallows where temperatures did not rise above 14°C, from April through October. However, in a still more northerly region, Northumberland Strait, but one where water temperatures reach a high level in summer, winter flounders were abundant in shallow water during May and June but were not numerous there as temperature increased above 15°C. In mid summer they were concentrated at depths of 8–12 fathoms (15–22 m) where temperatures were between 12 and 15°C.

Comparison of winter flounder movements in other regions supports the concept that distribution is controlled by temperature. For example, in the Long Island region, their offshore movement was shown to be a gradual dispersal with flounders leaving warmer inner bays first, but remaining within the cooler portions at quite similar depths much longer. Thus winter flounders moved out of Great South Bay by late April or early May but apparently remained close to shore just outside the Bay, on the outer coast of Long Island. Temperature conditions of these two adjacent regions contrast markedly. Shallow, enclosed Great South Bay warmed up early with little thermal stratification while on the outer coast thermal stratification was marked and temperatures at 4 fathoms (7 m) had only reached 16°C by August.

Farther north, in southwestern Nova Scotia, there was a marked contrast in the timing and direction of movements of winter flounders in St. Mary Bay and Pubnico Harbour. In St. Mary Bay where temperatures remained relatively low (similar to Passamaquoddy Bay) winter flounders were found in the shallows throughout the summer. In contrast, flounders moved out of Pubnico Harbour between mid May and mid June as temperatures increased to about 14°C, probably not to deeper water but to the cooler shallows of the open coast.

The fact that this species is concentrated between temperatures of about 12–15°C over a wide geographical range, the fact that its movements out of various bays throughout its range occur as temperatures reach about 15°C, and the fact that return movements to the bays in fall do not occur until temperatures drop to the same level, are good evidence that winter flounders have a preferred temperature range of 12–15°C.

Although a preferred temperature was not demonstrated under laboratory conditions, an upper incipient lethal of about 27°C was demonstrated. This is just slightly higher than the ultimate upper lethals for the following species: Pacific salmon group, *Oncorhynchus* (23.8 to 25.1°C—Brett, 1952); brook trout, *Salvelinus fontinalis* (25.3°C—Fry *et al.*, 1946); and lake trout, *Salvelinus namaycush* (23.5°C—Hart, 1952). Final preferenda for these species lie between 12 and 16°C according to a listing by Ferguson (1958) of the results obtained by various workers in laboratory experiments on preferred temperatures. According to Ferguson (1958) temperatures at which aggregations of these species occur in nature are in good agreement with the final preferenda determined in the laboratory for these species. A preferred temperature range of 12–15°C for winter flounder, derived from field observations, and an upper incipient lethal of 27°C appear to be consistent with the relationship between preferred and lethal temperatures for the salmonids.

SALINITY. Winter flounders are not found in fresh water but they tolerate salinities as low as 15‰ for long periods (Sumner, 1907). During the summer of 1948 a series of experiments was carried out to define the tolerance of winter flounders to low salinities. Exposure to water of 15‰ at temperatures of 13–14°C produced no deaths in two weeks of observations and confirms the statement of Sumner (1907). Flounders exposed to water of about 8‰ died in from 72 to 96 hours.

In general, for regions under discussion, salinities will not reach levels as low as 15‰. Movement from the shallows generally will take the flounder into higher salinities. However, the variation will not be great. For example, it may be between 25‰ near the head of Long Island Sound to 31.5‰ seaward of Block Island in May and June (Riley, 1952). Bottom salinities over this distance will change even less. The experiments of Bull (1936, 1938) with other flounder species suggest that winter flounders may be able to detect changes in salinity.

However, the seasonal cycle of changes in salinity will follow the same general pattern in the areas for which winter flounder distribution has been shown to be different. Salinities will be close to the same level about the same time of year, so variation in the summer distribution of the fish is not likely related to salinity.

LIGHT. In spring, for the areas shown in Table XIV, winter flounders are abundant in the region of higher light intensity. In summer, in areas of high water temperatures, such as Block Island Sound and Northumberland Strait, they move into regions of lower light intensity, while in areas of low water temperatures, such as Passamaquoddy Bay and St. Mary Bay, they remain abundant in regions of higher light intensity. Thus, their summer depth distribution throughout much of their geographic range is not consistently related to changing light intensity as it is related to temperature.

TABLE XIV. Occurrence of winter flounders in relation to light intensity and depth, shown schematically for four areas.

	Spring (April–May)		Summer (June–September)	
Place	Shallow water (higher light intensity)	Deep water (lower light intensity)	Shallow water higher light intensity)	Deep water (lower light intensity)
Block Island Sound	++	–	–	++
Passamaquoddy Bay	++	–	++	+
St. Mary Bay	++	–	++	+
Northumberland Strait	++	–	–	++

++ Abundant; + Numerous; – Few.

FACTORS AFFECTING FALL AND WINTER DISTRIBUTION

The reasons for movements of winter flounders in fall and their subsequent winter distribution are much more difficult to assess than those in summer. By early fall, winter flounders increased in numbers from a summer minimum within the bays and shallow water south of Cape Cod as temperature decreased there to about 15°C. However, it appears that only part of the population has returned to the bays and that they are found from shallow to deep water as was shown for Northumberland Strait in October and November. In fall the thermal stratification breaks down and the whole area from shore to where the winter flounder was found during summer is within the preferred temperature range. At any rate, winter flounders are found in the shallows and shore zone in early fall along the whole area in which their distribution was examined.

As winter begins the movements of winter flounders differ between north and south. In the north, flounders move deeper and become less abundant within the bays, while to the south (Long Island bays and Block Island Sound) they remain in the shallow water.

A similar divergence in winter distribution pattern is not uncommon for other groundfish species. Movement into deeper water off the Nova Scotia coast as winter approaches has been reported for haddock by Needler (1930) and for cod by McKenzie (1934). South of Cape Cod the same species are reported as moving westward and into shallower water during fall and winter (Schroeder, 1930; Needler, 1930).

Movement of winter flounders out of the shore zone of Passamaquoddy Bay and St. Mary Bay in fall and early winter appears as a gradual withdrawal, occurring after the summer temperature gradient has been reversed and the deeper water is warmer than the shallower, and after temperatures have dropped below the preferred range in the whole area. Withdrawal begins however at temperatures much higher than those found in the spring when flounders move into the shallow water. Movement out of the shallows north of Cape Cod occurs as temperatures decrease in fall rather than after reaching lower but more stable winter conditions.

Winter water temperatures south of Cape Cod are higher than those in the Canadian region, but in both regions temperatures alongshore are below the indicated summer preferred temperature range of winter flounders. In both regions inshore waters are colder than offshore. It might be expected that on the basis of temperature conditions flounders would move out of the bays of Cape Cod as well. However, mature flounders south of Cape Cod have reached spawning condition in early winter, while those in the northern region have not. The difference in behaviour pattern in winter between south and north may be related to the stage of gonad development. There is some evidence that immature flounders leave the immediate shore zone during winter months (Warfel and Merriman, 1944).

STRATIFIED DISTRIBUTION OF IMMATURE FISH

In Northumberland Strait in August large winter flounders were in deeper and small fish in shallower water (Fig. 10). In Long Island waters, Perlmutter (1939) showed that smaller, immature flounders did not move offshore as early in summer, and probably did not move as far as the larger fish. Such differential migration would bring about the type of size stratification found in Northumberland Strait.

In Passamaquoddy Bay a gradation in depth distribution is apparent for immature fish (Fig. 3) during summer, the smaller immatures being shallower, the larger deeper. However, in Passamaquoddy Bay the large, mature fish are found in the shallow water along with the smaller immatures.

In May 1948, in Pubnico Harbour, a similar stratification of immature fish with depth was apparent, while, like Passamaquoddy Bay, mature fish were most abundant in shallow water (Table XV).

The stratified distribution of winter flounders shown in Passamaquoddy Bay and Pubnico Harbour differs from that shown for Northumberland Strait and Long Island waters in two ways: First, the large fish are not most concentrated in deepest water, and second, the stratified distribution occurs at a time when water temperatures are at a relatively low level.

For Northumberland Strait and Long Island waters the differential distribution of fish according to size may be related to water temperature. As temperature increases large fish may be more influenced by the higher temper-

TABLE XV. Catch of immature winter flounders per drag by age and depth in Pubnico Harbour, May 19–21, 1948.

	Depth of tow	
	1–5 fathoms	6–8 fathoms
Age	Catch per drag	Catch per drag
	no.	*no.*
I	12.3	2.2
II	16.6	35.5
III	5.2	15.4
IV	1.0	3.5

atures than small fish. However, there are no data from this investigation to provide independent assessment of this possibility.

In Passamaquoddy Bay and Pubnico Harbour the differential distribution of immature fish apparently is related to some environmental factor other than temperature. The results of experiments with small and intermediate sizes of immature flounders and large, mature flounders suggest that their differential distribution results from the behaviour of different sizes of flounders in relation to light. In the experiments the immatures of intermediate size moved into shade with lower light intensities than small immatures. These results are in line with their distribution in Passamaquoddy Bay and Pubnico Harbour where small, immature fish were found in the shallows and the larger immatures deeper. Andrews (1946) showed experimentally a changing behaviour in relation to light for suckers, *Catostomus commersonii*, of different sizes (the smallest remaining in light of higher intensity), and correlated the results with their depth distribution in streams.

The gradation in depth distribution with size and age for immature flounders in Passamaquoddy Bay is similar to that reported by Johnson (1940) for herring, *Clupea harengus*, and by Huntsman (1942) for Atlantic salmon. In each instance the author has related the differential distribution to differential behaviour of the fish in relation to light.

The largest winter flounders used in the light experiments did not move into the shade with the same low increase of light at which the intermediate-size fish did. However, these two groups of fish differed both in size and sexual maturity, and it is not possible from these experiments to relate the change in behaviour specifically to either factor. The distribution of 3-year-old fish in Passamaquoddy Bay suggests that the change in behaviour is associated with sexual maturity. Thus, immatures of age III were concentrated in deeper water throughout the summer while matures of the same age and approximate size were almost equally abundant in both shallow and deeper water. That behaviour in relation to light may change at sexual maturity is suggested by the experiments of Lowe (1952) with eels, in which sexually-maturing eels avoided lighted areas more markedly than did the immatures.

Economic Implications in Canadian Waters

From Passamaquoddy Bay, N.B., to Cape Breton, N.S., the shallow-water belt is relatively narrow compared to that south of Cape Cod where extensive fisheries for the winter flounder have developed. Spawning concentrations in the shallows and concentration of the species between 12–15°C, when these temperatures are available, confine the fish to a narrow zone in these Canadian waters. While large catches were made in exploratory dragging they are probably not indications of large populations but of accumulated stocks which would only suggest short-term high levels of production. The high percentage of tag returns from the St. Mary Bay population supports this view.

It is suggested then that exploitation of winter flounders in this region will be limited to small local developments and that the population of flounders will support only limited commercial fisheries. Since winter flounders are found close to shore in many regions during the "good weather" months, a sport fishery could develop if interest increases.

In the southern Gulf of St. Lawrence, where usually the bottom slopes more gradually, water of the temperature at which winter flounders have been shown to be concentrated will cover a considerably wider zone. The fact that large catches have been made there within this temperature range may indicate a considerably larger population and thus better prospects of exploitation of the species on a continuing high level.

SUMMARY

The winter flounder, *Pseudopleuronectes americanus* (Walbaum), is found along the Atlantic coast of North America from Labrador to Georgia and is common in Canadian inshore waters.

Its depth distribution and movements are compared for representative areas from various parts of its geographic range and related to the environmental factors responsible for the seasonal changes in this distribution. In Canadian waters its distribution has been determined mainly by exploratory dragging, with some pertinent information obtained from small, recently-developed, otter-trawl fisheries. For waters off the United States its distribution has been obtained from accounts in the literature and deduced from published statistics of the commercial catch.

South of Cape Cod winter flounders regularly move out of the bays and shore zone during the summer months, while north of Cape Cod this offshore movement occurs in some regions but not in others. Where offshore movements occur in spring and summer they are correlated with an increase in temperature of the inshore waters to above 15°C. Where temperatures do not exceed this level winter flounders remain within the shore regions during the summer months.

In a number of regions they are most abundant between temperatures of from 12 to 15°C, although temperatures above and below this level are available. It is therefore concluded that this is the preferred temperature range for the species.

Lethal levels of temperature for flounders are well above the preferred range and in Canadian waters temperatures do not reach lethal levels.

Winter flounders are not found in fresh water and salinities of 8‰ are shown by experimentation to be lethal. Below-normal salinities of 15‰ at temperatures of 13–14°C have been shown experimentally to be within the zone of tolerance. Low salinity may act as a barrier but does not appear to direct their movements.

Winter flounders exposed to experimental light conditions showed different reactions. Larger immatures move into shade at lower light intensities than the smaller immatures. Large, mature flounders moved into shade at lower light intensities than small immatures but not at the same low light intensities as the larger immatures.

Where winter flounders are found in shallow water during summer, young, immature flounders occur in the shallowest water and older immatures relatively deeper. Mature flounders are abundant in the shallowest water but spread into the relatively deeper water also. Under these conditions this differential distribution with depth may result from a different behaviour pattern with size and maturity in relation to light.

South of Cape Cod winter flounders reappear within the bays in early fall after thermal stratification breaks down and temperatures return to the preferred range. However, distribution of the fish seems relatively diffuse and the return to the bays simply a spreading into space where high temperatures are no longer prohibitive. A similar movement in fall for more northern waters is suggested from distribution of flounder catches in Northumberland Strait, when temperatures of the inshore water had decreased to about 13°C in October and were almost isothermal.

In Passamaquoddy Bay winter flounders leave the shore zone for the deeper water of the Bay by November after the shallow water becomes colder than the deeper, but while temperatures are considerably higher than those in which winter flounders occur in spring.

A markedly decreased availability of winter flounders within Passamaquoddy and St. Mary Bays during the winter months has been shown. This withdrawal to deeper water as temperatures decrease and the shallow water becomes colder than the deeper appears common north of Cape Cod. South of Cape Cod a similar dispersal in winter does not occur even though it might be expected on the basis of similar winter temperature conditions. That flounders do not withdraw in the southern regions seems to be the result of the fact that mature fish are in a spawning condition there in mid winter. In northern areas immature winter flounders move deeper as temperatures decrease and available data, while neither precise nor extensive, suggest that they may also do so in southern areas. This suggested similarity of winter distribution for immature fish adds support to the conclusion that the dissimilar winter distribution of mature fish for south and north is related to the difference in their spawning condition.

Young flounders do not appear to migrate as far offshore as older flounders and this migration may occur later, whether migration occurs as temperature is increasing or decreasing. This may result from more rapid acclimation of young fish to changing temperature.

In the vicinity of Cape Cod the shallow water zone is broad and the large, sustained fishery there denotes a large population of winter flounders. Relatively good exploratory catches have been made in the Bay of Fundy and along the outer coast of Nova Scotia. In these regions, where the winter flounder is restricted to a relatively narrow shallow-water zone, these catches are probably not indicative of large populations, but of accumulated stocks. High catches are possible on a short-term basis but are not likely to be sustained. The southern Gulf of St. Lawrence is similar to Cape Cod in having a wide, shallow-water zone. The good exploratory catches in this area are suggestive of a large population of winter flounders and possibly longer-term exploitation.

ACKNOWLEDGMENTS

This study was suggested by Dr W. R. Martin whose advice and encouragement is gratefully acknowledged. I wish to express my appreciation to Drs F. E. J. Fry and J. R. Dymond of the staff of the Department of Zoology at the University of Toronto for their guidance and advice in the approach to this problem.

In preparation of this paper the suggestions received from Dr J. L. Hart are gratefully acknowledged.

It is a pleasure also to acknowledge the assistance given by other members of the groundfish staff of the Fisheries Research Board of Canada Biological Station, St. Andrews, in collecting samples, measuring fish, tagging and collecting tags. The assistance given by the boat crews of the various research vessels used during the course of this study is gratefully acknowledged.

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NOTES

Downstream Movements of Brook Sticklebacks, *Eucalia inconstans* (Kirtland), in a Small Southern Ontario Stream

From the fall of 1957 through to December 1959, a study of sea lamprey (*Petromyzon marinus*) and rainbow trout (*Salmo gairdneri*) was carried out in Silver Creek, which flows into southern Georgian Bay (Lake Huron) just west of the town of Collingwood. Parts of these data have been previously summarized (Lamsa, 1961), but no mention was made of the rather spectacular downstream movements of brook sticklebacks which occurred each spring.

Little information appears to be available on the movements of brook sticklebacks in streams. Winn (1960) states, "characteristically the brook stickleback migrates into shallow water to spawn in the spring, after which it gradually moves to deeper water or downstream in the summer". Applegate (1961) records, for most months, half-monthly totals of downstream runs of brook sticklebacks[1] for 10 years in Carp Lake River, Michigan. The Silver Creek data, although superficially similar to the Carp Lake River data, are, on the other hand, sufficiently different to warrant recording.

Silver Creek, 7$\frac{3}{4}$ miles (12.4 km) long, with a normal summer flow of approximately 10–15 cubic feet (280–420 liters) per second, arises as a spring-fed stream on top of the section of Niagara escarpment called the Blue Mountain. The stream drops over 970 ft (296 m) before entering Georgian Bay, most of the drop occurring in the upper 3$\frac{1}{2}$ miles (5.2 km) of stream. The remainder of the stream is more gentle, consisting mostly of gravel riffles and pools, but half a mile from Georgian Bay it forks into two branches which separately enter the lake. The western branch, which carries over half the total flow, meanders through alder and willow swamp, while the eastern branch courses through fields.

All-metal fish traps, designed to catch fish moving upstream and downstream throughout the year, were installed in March 1958, one in each branch about a quarter mile (0.4 km) from the mouth. Flattened, expanded metal lath with $\frac{1}{4}$-inch (0.63-cm) mesh was used to cover the trap in the western branch; $\frac{1}{2}$-inch (1.27-cm) mesh of the same material was used on the other trap. Both traps were operated continuously from the time of installation to December 1959, being inoperative only during periods of flooding, but no floods occurred from approximately mid May to approximately mid July either year.

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[1] The fish in the report is listed as the threespine stickleback, *Gasterosteus aculeatus* L., but the author has verified the species as the brook stickleback, *Eucalia inconstans* (Kirtland) — personal communication from the author.

J. Fish. Res. Bd. Canada, **20**(2), 1963.
Printed in Canada.

The downstream movements of sticklebacks are shown in Table I. All these fish were caught in the trap in the western branch. None were caught in the trap in the eastern branch. Since the latter trap was covered with ½-inch (1.27-cm) mesh, some sticklebacks could have escaped through undetected, but it is unlikely that any quantity of sticklebacks could have done so without some being caught in the screen or trap. The presence of sticklebacks in one trap but not in the other suggests that these fish may have originated in the ¼-mile (0.4-km) section between the forking of the stream and the trap.

TABLE I. Downstream movements of brook sticklebacks in 1958 and 1959.

1958		1959		
Date	No. of brook sticklebacks	Date	No. of brook sticklebacks	Mean water temp.
				°C
Mar. 25[a]–31	2	Jan.–Mar.	0	. . .
Apr.	0	Apr.	14	. . .
May	10	May 1–30	2	. . .
June 1–7	35	May 31–June 6	1	15
June 8–14	2851	June 7–13	11	18
June 15–21	46	June 14–20	22	13
June 22–28	36	June 21–27	11	16
June 29–July 5	10	June 28–July 4	908	19
July 6–12	43	July 5–11	87	18
July 13–19	10	July 12–18	76	18
July 20–31	0	July 19–25	43	18
Aug.–Dec.	9	July 26–31	14	. . .
		Aug.–Dec.	2	. .

[a] Date trap installation completed.

The downstream movement of sticklebacks was more spectacular in 1958, when a total of 3052 fish were counted downstream. Of these, 2851 (93%) were caught in a single week, 1324 sticklebacks being the most caught in one day. No water temperature data are available for this period. Few sticklebacks were caught in the fall, although occasional floods at that time of year could have carried some downstream undetected.

In 1959 the principal downstream movement occurred much later, at the end of June and early July, when 908 sticklebacks (76% of the total run of 1191) were caught in one week. The weekly mean water temperatures for June and July, taken by a recording thermometer, are shown in Table I. As in 1958, few sticklebacks were caught in the fall, but occasional flooding could have enabled some to pass over the traps.

Few sticklebacks were caught moving upstream. In this respect, they differed from some of the minnows which showed movement both ways. In 1958 only 3 sticklebacks were caught moving upstream, and in 1959 only 4 were so caught.

The Silver Creek data differ from the Carp Lake River data in the time of spring that the run began and its duration. In Carp Lake River, Michigan, the downstream movement began in early April, and by the end of May most of the sticklebacks had been passed downstream. In addition, the run was not concentrated, but generally was spread over the entire season. In Silver Creek, the sticklebacks did not begin to move downstream in any abundance until June, and then the run was concentrated so that most of the fish went through the trap in a week.

Fisheries Research Board of Canada
Biological Station, London, Ont.

A. Lamsa

Received for publication August 29, 1962.

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